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**RELATIONSHIPS OF THE
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ALECTOROMORPHAE AND
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PUBLICATIONS OF THE NUTTALL ORNITHOLOGICAL CLUB, No. 17
Editor, Raymond A. Paynter, Jr.

RELATIONSHIPS OF THE SUPERORDERS
ALECTOROMORPHAE AND CHARADRIOMORPHAE
(AVES):
A COMPARATIVE STUDY OF THE AVIAN HAND

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CONTENTS

FOREWORD <i>by</i> Walter J. Bock	1
INTRODUCTION	9
ACKNOWLEDGEMENTS	15
SYSTEMATIC OBSERVATIONS	17
TINAMIFORMES	17
GRUIFORMES	22
RALLIDAE	22
GALLIFORMES	28
CRACOIDEA	29
MEGAPODIIDAE	29
CRACIDAE	32
PHASIANOIDEA	34
PHASIANIDAE	34
MELEAGRIDIDAE	37
NUMIDIDAE	37
TETRAONIDAE	38
DISCUSSION	38
CUCULIFORMES	40
MUSOPHAGIDAE	40
CUCULIDAE	44
OPISTHOCOMIFORMES	52
GRUIFORMES	57
TURNICIDAE	57
OTIDIDAE	61
GRUIDAE	64
EURYPYGIDAE	67
CARIAMAE	69
CARIAMIDAE	69
PSOPHIAE	72
PSOPHIIDAE	72
CHARADRIIFORMES	75
CHARADRII (LIMICOLAE)	75
CHARADRIIDAE	75
Charadriinae	76
Vanellinae	78
Calidridinae	78
Tringinae	78
Scolopacinae	79
DISCUSSION	80
GLAREOLIDAE	80
BURHINIDAE	81
JACANIDAE	83
CHIONIDIDAE	86

CONTENTS

THINOCORIDAE	89
LARI	91
STERCORARIIDAE	92
LARIDAE	94
STERNIDAE	95
RYNCHOPIDAE	96
DISCUSSION	97
ALCAE	97
ALCIDAE	97
DISCUSSION	100
COLUMBIFORMES	100
COLUMBIDAE	101
PTEROCLIDIDAE	105
DISCUSSION	108
PSITTACIFORMES	109
SUMMARY	115
LITERATURE CITED	117

FOREWORD

While correcting and editing the English translation of Professor Stegmann's manuscript, I was repeatedly struck by his insights into the fundamental ideas and methodologies of systematics. However, many of these ideas may be obscured because of the manner in which they are expressed and by the lack of references to recent literature on systematic theory and methodology, much of which lies outside of the ornithological literature and much of which was presumably unavailable to Professor Stegmann. I was often tempted to insert editorial comments and to use newer terms, but felt restrained because I believe that the published paper should reflect, as truly as possible, Professor Stegmann's thoughts and arguments. I have, however, summarized my comments in this foreword, hoping to couple the ideas and expressions used by Professor Stegmann with those that may be better known to English-speaking ornithologists. For brevity, I shall not provide extensive citations for the ideas discussed, most of which can be found in my reviews of "The avian skeletomuscular system" (Bock, 1974), and of evolutionary classification (Bock, 1977), which includes reference to most of the pertinent literature. Moreover, this foreword may serve to introduce Stegmann's earlier studies in avian systematics as well as being a brief introduction to work on the morphology of the avian wing.

Professor Stegmann has written on the systematics of the orders of alectoromorphous birds since the early 1950's, with greatest attention being given to the question of the relationship of the sandgrouse (Pteroclididae) to either the Columbidae or to the Charadriiformes. A discussion, including extensive literature citation, of sandgrouse/pigeon relationships has been presented recently by Fjeldså (1976, 1977). Stegmann's analysis was based upon a broad comparative anatomical study, which gradually focused on wing structure and finally led to the study reported upon in this paper. Choice of the distal tip of the wing—the skeleton and musculature of the hand—was, without doubt, the most brilliant decision in the study. Most earlier investigations of avian relationships were based upon comparative anatomical studies of the skeletomuscular systems of the head and hind limb. Professor Stegmann seized upon a virtually unknown set of taxonomic features and turned them into valuable evidence supporting ideas of relationships and classification of a major group of avian orders.

Good taxonomic features must possess several properties. First, the features must exhibit sufficient variation at the proper taxonomic level for the systematic questions being asked; too much variation reduces the value of a taxonomic character as much as too little variation. In this publication the relationships between orders and suborders of birds are the primary questions being asked, with the relationships between families and subfamilies of minor concern. The second property of good taxonomic features is that they must be preserved and stored with a minimum of distortion. This allows broad comparative surveys to be undertaken. The third, and last, property is that the features

FOREWORD

should be well enough known biologically to permit studies of function and ecology which are necessary in order to interpret the adaptive and paradaptive attributes of these features and to trace their evolution. The avian hand fulfills all these requirements.

Stegmann developed a method by which the hand could be extracted from a study skin and the ligaments and muscles softened in order to be examined. Material obtained in this manner is almost as good as material from a specimen preserved in formalin. By using this method a broad selection of taxa could be obtained from study skins, thus avoiding the usual frustrations of the avian morphological systematist who frequently finds he lacks the critical taxon needed when making comparisons.

In basing his work on the pioneering monograph of Fürbringer (1888) and on the later paper by Sy (1936), Professor Stegmann was well aware of the relative uniformity shown by the shoulder region in contrast to the variation displayed by the hand. He, therefore, made use of the distal tip of the wing, rather than the proximal (shoulder) end, thus insuring that sufficient variation would exist between groups. His decision is well supported from a functional morphological argument, as well as one based on natural selection. For example, movements of the humerus relative to the shoulder are restricted and simple. Moreover, elements of the shoulder region interact in a number of different functions, and must, therefore, have a morphology that is a compromise between these conflicting functions and selective demands. Both of these factors restrict the amount of morphological modification of the shoulder that can accompany the evolution of a new group with a different mode of flight. However, quite the opposite holds for the hand. It is isolated structurally from other anatomical systems and hence its evolutionary change is less restrained by compromising influences. Furthermore, control of flight is achieved by movements of the primaries for which subtle adjustments of the underlying bones may be required. Thus, differing modes of flight may well be best reflected in the morphology of the hand. The history of variation, and that of the selection forces (indicating the environmental changes) that chose particular variations, may be determined more readily from morphology of the hand than from any other part of the wing.

Systematists have, traditionally, shied away from features showing considerable variation between groups, as well as from those whose adaptive meaning is clearly evident. Instead they have favored more uniform, conservative features. I believe the real success of Professor Stegmann's analysis, and what makes it of especial interest, can be attributed to the fact that he chose a more daring course and selected a feature that has been ignored by other avian systematists.

Stegmann's analysis of the alectoromorphous birds developed from his earlier considerations of the sandgrouse. Limits had to be placed on both the morphological and taxonomic scope of the analysis. For the latter limit he chose the Legion Alectoromorphae, one of Gadow's (1893) four major subgroups of carinate birds. The Alectoromorphae include the following orders recognized by Wetmore: the Tinamiformes, the Galliformes (including the

FOREWORD

Opisthocomidae), the Gruiformes, the Charadriiformes, and the Columbigiformes. The Cuculiformes and the Psittaciformes, which Stegmann also includes in his study, are placed by Gadow together in the Order Cuculiformes within the Legion Coraciomorphae. Unfortunately, Stegmann did not include the Ratites, which are now recognized to be monophyletic and closely related to the Tinamiformes (e.g., Bock, 1963), and the Anseriformes, which some workers (e.g. Bock, 1970) believe to be closely allied to the Galliformes. With these exceptions, the taxonomic limits chosen by Stegmann are natural ones.

Stegmann began his work where Gadow left off. The gap of 85 years between the publication of Gadow's monograph and Stegmann's study testifies to the dearth of taxonomic work on relationships between avian orders. Almost no lasting study has been done in this area since Gadow's publication of 1893. The classifications of Wetmore, 1960, of Mayr and Amadon, 1951, and of other modern authors are based almost exclusively on Gadow's ordinal classification. Stresemann (1927-34; 1959) recognizes many more orders and appears to differ sharply from Gadow, but actually even his system is fundamentally the same because most of his orders are equivalent to the suborders recognized by others (e.g., Wetmore).

Stegmann makes a clear distinction between the problem of ascertaining evolutionary changes between groups of birds, which he does by considering both the pattern of phylogeny and the amount of modification, and the problem of grouping taxa into groups of varying categorical rank. When comparing characteristics of taxa, Stegmann distinguishes between the types and directions of evolutionary change, and whenever possible identifies primitive features and groups. Although he treats parallel evolution and convergence, possibilities such as reversals and secondarily primitive conditions are overlooked.

Stegmann begins with a series of hypotheses regarding relationships which he expresses in Gadow's system. He then tests them against the empirical evidence derived from his own comparative morphological study. Because of the language and the mode of expression used, it may not be clear to the reader that Stegmann follows this approach; careful reading is necessary to recognize it. Under the *Thinocoridae*, for example, he says that the "Anatomical characters of *Attagis* are too neutral . . ." for determining exact relationships. This statement may appear vague at first glance. It may, however, be translated to mean that these features do not show distinct attributes that provide good tests of any reasonable hypothesis of relationships between *Attagis* and possible close relatives within the Charadriiformes. Moreover, Stegmann clearly realizes that different types of comparative evidence are of varying value in treating taxonomic hypotheses, and that these values may be assessed by a functional/ecological study of the characters.

The most significant aspect, I believe, of Stegmann's character analysis is his recognition of the importance of both functional as well as ecological factors. Unfortunately, his discussion of these topics is too brief and is

FOREWORD

based on only a few direct observations of function and detailed field studies. Statements about function are mainly a synthesis of observations on morphology and general comments about the flight characteristics and life history of the bird (e.g., the rapid, vertical take-off of the quail). The discussion of the roadrunner (*Geococcyx*; Cuculidae) is a good example of the depth of analysis achieved from fairly simple field observations. Although Stegmann's functional analysis is only a beginning, it is clearly in the right direction in that it emphasizes the significance of functional-adaptive character analysis in serving as a foundation for morphological-systematic studies.

Stegmann usually considers function in the sense of biological role (Bock, 1974), but his meaning is clear in most cases. He always discusses adaptations in terms of each taxon's environment (frequently broadly stated) and often in the light of the history of the group. Good examples of these discussions may be found under the account of *Opisthocomus* and that of *Chionis*. In the latter, for instance, he suggests that *Chionis* evolved on a continental land mass and adapted to ecological conditions found there, but now is a relict on subantarctic oceanic islands.

Throughout his discussion of function and adaption, Stegmann appreciates that a balance, or a compromise, often exists in the morphology of a structure because of functional requirements or because of conflicts between various selection forces. This is nicely documented in the discussion of the suite of peculiar specializations in the alcid wing, which have resulted from the necessary compromises between the differing positions of the wing in aerial flight and in underwater swimming. A further example is shown when in describing the wing of the Rallidae, Stegmann states that the muscles cannot be strong if the bones are weak, and hence these birds have a generally weak flight apparatus that precludes certain types of flight, such as rapid take-offs. His sensitivity to the role of balance is further shown when he notes that in the Charadriiformes, as in *Chionis*, there is a decrease in size of the *M. flexor digitorum superficialis* when there is an increase in size of the *Lig. humero-carpale*.

All evolutionary modifications in the wing tip, as well as those of other systems considered in this paper, are considered against a background of avian flight. The reptilian set of hand muscles and quadrupedal locomotion are accepted as the general beginning reference point, although Stegmann is well aware that the Tinamidae, the most primitive group of birds within the complex studied, is well advanced over the reptiles. Many of the changes are reduction series, such as the loss of terminal phalanges or of parts of multiple muscle insertions or of whole muscles. It is argued that these reductions or losses result in flight movements which are simpler than reptilian quadrupedal locomotion. The maximum of 18 reptilian muscles is reduced to a minimum of 12 in the most advanced birds, but not all birds lose the same muscles. Most interesting is that the muscles with duplicated functions are lost and these are always muscles that cross only one joint rather than traverse two joints (see also, Bock, 1974). Stegmann tends to use such reduction series as evidence of the direction of evolutionary change and as an indication

FOREWORD

of how far the taxon has advanced. He clearly realizes, however, that reduction series are not nearly so useful in delimiting groups and in documenting relationships between them.

The appearance of specializations is the second main type of evolutionary change studied by Stegmann. He stresses their great value in delimiting taxa and in showing affinities between them, especially when the specializations are evolutionary novelties. Examples of these specializations are found in the Lig. spirale in pigeons and the insertion of the M. flex. dig. superficialis on metacarpale III, not II, in guinea fowl (a condition made possible only with the evolution and subsequent loss of the muscular tuberosity). As far as possible, Stegmann provides the reasons supporting his beliefs why certain specializations are uniquely derived features and hence most useful taxonomically.

Features are analyzed to determine whether they are primitive or advanced, but again the reader must be aware of the different terms used by Stegmann to designate these states. For example, he uses phrases such as "phylogenetically old" to mean "primitive" and "newly acquired" to mean "advanced". It is important to recognize that these designations are not unsupported decisions, but rather are based upon comparisons with reduction series or by determining which features probably represent evolutionary novelties. Much of the analysis is founded on the premise that the morphology of tinamous is primitive. This is presumably based upon the concept that among living birds the palaeognathous birds are primitive. While it is true that the tinamous are the basic stock for palaeognathous birds, cranial evidence suggests that ratite radiation is really indicative of an advanced group of birds with its origin later than that of many other avian orders (Bock, 1963; 1964). Thus, primitive conditions in wing morphology may have to be looked for in other avian groups, and the apparent directions of some of the evolutionary changes may have to be reversed. Yet even if the basic premises of Stegmann as they relate to the primitiveness of groups or of characteristics are incorrect, the bulk of the analysis and the taxonomic conclusions will be little affected. More seriously affected, however, may be conclusions about phylogenetic relationships between taxa.

Stegmann appreciates clearly that the adaptiveness and the taxonomic value of a feature are not mutually exclusive properties. Although he does not use terms such as "multiple pathways of evolution" and "paradaptations" (Bock, 1967), Stegmann employs these concepts extensively. He shows that various structural conditions represent different modes of adapting to the same general selection force, that the same biological roles are involved, and that such features are especially valuable in testing relationships. One example is the several structural methods that maintain the curvature of the tendon of the M. ext. dig. communis just before its insertion. The evolution of the muscular tuberosity and its associated M. ulni-metacarpalis dorsalis appears to occur in two distinct patterns, one in gallinaceous birds and one in *Turnix* and its relatives. The bearing on this study of these ideas of multiple evolutionary pathways is most clearly shown by Stegmann's discussion of

FOREWORD

the major differences between the Galli and the Rallidae, which are recognized by him as the basal members of the two major adaptive radiations, the Alectoromorphae and the Charadriiformes.

The major taxonomic conclusions presented by Professor Stegmann generally support those of Gadow, and hence the currently accepted system, but with some notable exceptions. Stegmann recognizes two superorders, the Alectoromorphae and the Charadriomorphae, which are the natural divisions of Gadow's Legion Alectoromorphae. The greatest modification is in the removal of Gadow's Cuculiformes from his Legion Coraciomorphae and its division into the Cuculiformes and the Psittaciformes. The former group is placed in the Alectoromorphae, with the Musophagidae being more closely allied to the Galliformes. The latter group is placed in the Charadriomorphae with affinities to the base of the Columbidae. The second major change is the removal of the Cariamidae and the Psophiidae from the Gruiformes, and their placement as taxa incertae sedis at the base of the Alectoromorphae. These families may have some distant affinities to one another; these conclusions agree with the doubts expressed by Cracraft (1973:116-117) on the position of the Psophiidae. Stegmann has excellent discussions of problem groups, e.g., the Opisthocomidae (see also Sibley and Ahlquist, 1972, 1973) and the Pteroclididae, which he had studied earlier (see Sibley and Ahlquist, 1972; and Fjeldså, 1976). For these problem taxa, Stegmann demonstrates clearly that each taxon shows affinities to the several groups to which each had been allied by earlier ornithologists, and that the analysis of their correct relationships is not a simple task. Simple sets of evidence could well provide misleading clues to their affinities. Quite possibly these problem taxa evolved from their nearest relative close to the point of divergence between the two taxa to which they have been allied (e.g., the Columbidae and the Charadriiformes for the Pteroclididae).

Professor Stegmann has made a valuable contribution to systematic ornithology by introducing a new anatomical system, with many potentially valuable taxonomic characters, and by examining the affinities of several orders containing 1,700 of the 3,750 species of nonpasserine birds. His study is not presented as a final analysis, but as an introduction—and a most splendid one. The taxonomic survey must be broadened to embrace the remaining avian orders. Also, and of greater importance, a more detailed functional as well as biologically oriented morphological investigation of the wing tip must be undertaken to provide the basis for a more complete taxonomic analysis of the many useful characters found therein. With the rapidly expanding knowledge of avian flight being provided by Pennycuik, Greenewalt, Oehme, Tucker, and Nachtigall (Tucker, 1975; Pennycuik, 1975), it should be possible to replace the present speculations on function with sound empirical observations.

It is regrettable that Professor Stegmann was not able to begin his studies of the avian hand early in his distinguished career, and that his death on 28 December 1975 occurred prior to the publication of this outstanding study, the manuscript of which he completed in mid-1971. However, ornithologists

FOREWORD

should be grateful to Professor Stegmann for his excellent introduction to comparative morphological and systematic investigations of the avian hand.

The painstaking translation to English from the German of Dr. Stegmann's original manuscript was undertaken by Gretel Mayr. Dorothea Goldys skillfully touched up and relabelled the drawings and arranged them into the figures used herein.

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FOREWORD

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INTRODUCTION

All the characteristic anatomical features of birds are the result of adaptations to flight. The most important adaptation has been the modification of the anterior paired appendages from legs to wings, but the influence of flight also can be seen throughout the avian body. Moreover, various environmental influences cause different species to have different modes of flight. This, in turn, means that the size, shape, and proportion of the wing also varies considerably, because, obviously, the type of flight has great influence on the structure and shape of the wing. Parallel evolutionary development may be seen clearly in unrelated groups of birds that have adapted to a similar way of life, and hence of flight, independent of each other. One need only be reminded of the similarity in wings of swallows, swifts, and petrels. For these reasons the external morphology of the avian wing cannot be used for the purpose of classifying birds.

Fürbinger's detailed investigation (1888) of the pectoral girdle of birds served as the basis for his conclusions on the relationships of birds, and for the system of avian classification later proposed by Gadow (1891–1893). However, for several decades following these classic publications, no one followed through with a study of the distal portion of the wing. Only in 1936, when Sy published his specialized and very detailed investigation of the functional morphology of the skeletomuscular structure of the wing, was the distal segment finally treated. The foundation provided by Sy could have served as a beginning for comparative studies of the avian manus, but such studies did not appear until many years later. When I developed an interest in the distal segment of the wing, about a decade ago, it was clear that comparative study of the functional morphology of the avian hand was a new and fertile field of research.

Considering the entire morphology of the wing, one would expect that its internal anatomy would be less variable than its external form because the latter is more easily modified by the environment than the former. And this is usually the case, for when comparing several groups of birds, one often finds that the shapes of their wings vary widely, while the internal morphology of the wings is identical, or very similar. On the other hand, there are cases in which the external structure of the wing is similar in groups that have extensive differences in internal morphology. Therefore, a comparison of the external structure of the wing with its internal morphology in many different birds could provide a basis for further inquiry into the adaptive evolution of the avian wing.

Because so little was known about the morphology of the hand in birds, the essential first step in my study was to investigate as many avian orders and families as possible, with emphasis on species with different modes of flight in each group. Skeletons and alcoholic specimens of palaearctic species were readily available for this study, but only occasionally were specimens of exotic species. Fortunately, using a simple technique the wing

INTRODUCTION

of a dried museum skin can be softened, making the bones, tendons and ligaments available for study. The muscles regain their normal configuration too and are also available for investigation, because the muscles of the distal segment of the wing are only partly removed in study skins. Furthermore, only the hand and primary feathers of one wing are used, leaving the specimen essentially intact for almost all other observations normally made on museum study skins. Thus, even in the absence of traditional anatomical specimens I still could conduct my comparative morphology study.

Colleagues in foreign countries kindly assisted by sending me specimens that were poorly labeled or defective but which made valuable preparations for me. It was always an exciting moment to dissect a freshly softened specimen and to discover whether the original collector had prepared it poorly or well; my success depended on a rushed or lazy preparator. As collectors and museum curators know, all fleshy parts should be removed when preparing a museum skin. Therefore, in well-made skins my gain was small, but I was rewarded when the specimens were poorly prepared.

With the addition of preparations from study skins, I was able to assemble a collection of the manus portion of the wing which permitted an extensive comparative study. Only by comparing a large number of species could I solve some of the essential questions of functional morphology that had to be answered before proceeding to phylogenetic assumptions.

The misconception is widely held that only those characters that possess no functional significance can be used for systematic conclusions (but also see Bock, 1967). Almost all characters are adaptations to different environmental factors, and if these characters are ignored, very little of the organism would be available for taxonomic research. In comparative analyses one can determine whether the function of a structure has remained the same or has been modified and, if modified, in what direction and under what set of circumstances. Thus, it may be possible to ascertain whether the features being studied are newly evolved or are phylogenetically old. In some cases it is possible to conclude whether the similarity of a feature in different groups is due to convergence, or whether a recent evolutionary change has occurred in the organism resulting in a dissimilarity that may conceal an actual relationship.

The material collected from skeletons, spirit specimens, and study skins enabled me to undertake a comparative investigation of the skeleton of the hand (manus of the wing), some of the major ligaments in the hand, and the muscles, including the tendons, which attach to and move the hand and the individual digits. The lack of suitable material and time prevented a comparative analysis of the complex system of ligaments found in the wrist, hand, and digits. I also had to exclude from consideration the bones of the wrist and could not give proper attention to the shapes of the articular surfaces, although it became obvious early in the study that their morphology is strongly modified in different groups of birds.

Eighteen muscles are included in the comparative study. Of these, five

INTRODUCTION

originate from the distal end of the humerus by a short tendon, four from the lower arm (radius and ulna) by a fleshy attachment, one from the lower arm by a short tendon, and the remaining eight from the carpometacarpus. The complete set of hand muscles is found in all old or "primitive" (= less highly evolved or advanced) groups of birds in the lower part of the system of avian classification. The only exception is the *M. flexor pollicis* that appears to be absent in some of the oldest groups. At the higher levels of avian classification, however, in groups such as the Coraciiformes and the Passeriformes, several hand muscles disappear, although not always the same ones. The minimal number of hand muscles in flying birds is twelve, the characteristic number for many passerines.

An explanation of this trend toward the loss of muscles of the hand may be outlined as follows. Because the avian wing evolved from the pectoral appendage of reptiles, the reptilian hand musculature may be considered as the primitive condition from which the muscles in birds are derived. But the movements of the wing are far simpler than those of a reptilian foot, such as that of the archosaurian ancestor of birds, which is adapted for running, climbing, or handling food. With simplification of the structure of the wing and its associated movements, some of the hand muscles duplicated partly or completely the actions of other muscles. With increasing evolutionary specialization the redundant muscles were eliminated by selection.

The lost muscle of a pair of redundant muscles is always the one that spans one joint (a one-joint muscle is one that rotates one bone, considering the site of origin as stationary) if the other muscle spans two articulations (a two-joint muscle is one that rotates two bones, considering the site of origin as stationary) (Stegmann, 1970). The reason for the loss of the one-joint muscle and the retention of the two-joint muscle appears to be that evolutionary changes are toward simplification of flight movements and, as far as possible, toward automation of several actions. The coupling of movements at the elbow joint with those at the wrist, which would result from the action of two-joint muscles, would be an advantage for many flight motions and would eliminate the need for individual muscular actions at each joint. See, also, the discussion of the advantages of two-joint muscles in Bock (1974:201–220), which is in agreement with this explanation.

In this paper I shall describe briefly the findings of my comparative morphology investigation of the distal part of the wing in several orders of birds. The comparisons of the hand morphology are, in essence, limited to the orders grouped together as the Alektoromorphae by Gadow, and my taxonomic conclusions are confined to these orders. I follow the classification of birds proposed by Wetmore (1960), which corresponds well with the earlier systems of Fürbringer and of Gadow. In this study I have not referred to the numerous treaties on avian classification published since Fürbringer and Gadow, and especially those published during the past three decades (since the end of World War II) for two reasons. First, a comparison of all the diverse schemes of avian classification would take too much space and,

INTRODUCTION

second, only a part of the classification of recent birds is treated herein. An elaborate discussion of a segment of the classification of birds would result in many confusing and misleading statements. I hope to be able to extend my comparative study of the hand morphology to all avian groups, after which I can discuss the entire system of avian classification based on this set of anatomical features.

The sequence of taxonomic groups used in presenting the morphological results does not always correspond to the system that I accept and would advocate. Rather, the sequence is the one most suitable for comprehending the peculiarities of the wing in different birds, their evolutionary modifications, and the comparative anatomical-taxonomic conclusions derived from the wing morphology.

The skeleton, musculature, and ligaments of the hand have been illustrated in dorsal and ventral views for representative genera from most of the taxonomic groups included in this study. The illustrations are of comparable views. Individuals bones and ligaments are labeled on the drawings in which they first occur. Because the number of names for bones and ligaments is limited, it is not necessary to list them in a table. The muscles are more numerous and complex, and I have chosen to label them by numbers rather than by names or abbreviations. The muscles and their numbers are listed below. To simplify comparison with recent literature, page reference is included in parentheses to the descriptions of these muscles in the study by George and Berger (1966), as well as to the names used by those authors in case of differences. The muscles of the carpometacarpus and the digits of the avian wing are:

- (1) *M. extensor metacarpi radialis* (pp. 357–359)
- (2) *M. extensor pollicis longus* (pp. 369–370)
- (3) *M. flexor carpi ulnaris* (pp. 354–355)
- (4) *M. flexor metacarpi ulnaris* (= *M. flexor digitorum superficialis*; pp. 347–352)
- (5) *M. ulni-metacarpalis ventralis* (pp. 356–357)
- (6) *M. ulni-metacarpalis dorsalis* (pp. 370–371)
- (7) *M. extensor digitorum communis* (pp. 361–363)
- (8) *M. extensor indicis longus* (pp. 365–368)
- (9) *M. flexor digitorum sublimis* (= *M. flexor digitorum superficialis*; pp. 347–352)
- (10) *M. flexor digitorum profundus* (pp. 352–354)
- (11) *M. abductor indicis* (pp. 375–376)
- (12) *M. flexor digiti III* (p. 379)
- (13) *M. interosseus dorsalis* (pp. 376–377)
- (14) *M. interosseus palmaris* (pp. 377–379)
- (15) *M. adductor pollicis* (pp. 373–374)
- (16) *M. extensor pollicis* (= *M. extensor pollicis brevis*; pp. 371–372)
- (17) *M. abductor pollicis* (pp. 372–373)
- (18) *M. flexor pollicis* (pp. 374–375)

The reader is referred to George and Berger (1966) for a description of the actions of these muscles, for additional references to the literature on

INTRODUCTION

the musculature of the wing, and for a discussion (pp. 226-227) of the problem in numbering the avian digits and the resulting confusion in the nomenclature of the muscles to these digits. The digits in this study are regarded to be the pollex (digit I), digit II, and digit III, as accepted by George and Berger (1966:226) and most other avian anatomists.

ACKNOWLEDGEMENTS

For kind gifts and the exchange of valuable foreign material essential for my comparative studies, I wish to extend my appreciative thanks to numerous colleagues including Dean Amadon (American Museum of Natural History, New York), Eva Grossmann (Histologisch-Embryologisches Institut der Universität Wien), Gottfried Mauersberger (Zoologisches Museum und Institut für spezielle Zoologie der Humboldt Universität, Berlin), and Helmut Sick (Museu Nacional, Universidade do Brasil, Rio de Janeiro). Lastly, I wish to thank the officials of the Zoological Institute of the Academy of Sciences (Leningrad) for permission to dissect material from the large collection of palaearctic birds, as well as from a collection of about 200 foreign birds preserved in alcohol. Shortly before the completion of this study I received several specimens of *Chionis alba* through the kindness of E. Grusow and I was able to include this interesting genus in the comparison.

I wish to offer special thanks and gratitude to the late E. Stresemann for his valuable advice and assistance that I shall always remember.

SYSTEMATIC OBSERVATIONS

TINAMIFORMES

Introduction.—The tinamous are a small group of peculiar, chicken-like birds, widely distributed over Central and South America. They are exclusively ground-dwellers, occurring in forests as well as in open country and underbrush, and lead a secluded existence hidden in bushes and high grass. They fly only short distances, but this is characterized by a rapid vertical take-off (high acceleration); this trait was developed at the expense of other types of flight. The tail feathers are short and hidden under the coverts. It has been assumed that the flight of tinamous is awkward and clumsy, but recent observations have shown that the forest species have an adequately maneuverable flight (Lancaster, 1964).

Species studied.—*Tinamus solitarius*, *Rhynchotus rufescens*, *Crypturellus noctivagus*, *C. tataupa*.

Description.—The wing of tinamous is short, strongly rounded, with very stiff flight feathers. The first primaries are narrowed at their tips, having been modified into propulsion feathers. There are 10 primaries, without a vestigial 11th. The secondaries are eutaxic.

The bones of the wing are short and strong, which is particularly conspicuous in the hand region (Fig. 1A, B). Metacarpus II is thick and oval in cross section so that the largest diameter is dorso-ventrally directed. It is bent in a characteristic forward and downward (radial and ventral) direction (Fig. 1A). Very peculiar is the absence of the distal process of metacarpus II; the bone terminates distally only in a lump that delimits the bone radially and also partly dorsally and ventrally. The bony groove for the insertion of the tendon of the M. ext. dig. communis is indicated only slightly in the distal part of metacarpus II.

The first digit has a well-developed second phalange with a pointed claw, the second digit has a small, but well-developed, third phalange. The first phalange of digit II is large, very broad in its distal part, with a strong bulge at the proximal end close to the ulna. Phalange II of digit II is broadly flattened dorso-ventrally, with a peculiar radical extension which permits the tendon of the M. inteross. palmaris to be well-separated from the phalange. This peculiar trait is not found in other birds. Digit III is comparatively short, flattened dorso-ventrally, and has a well-developed appendage.

The muscles of the lower arm are very strongly developed, giving the wing a fleshy appearance similar to that in gallinaceous birds (Fig. 7). Moreover, all muscles are long with short tendons. The tendon of the M. ext. metacarpi radialis is broad and flat, similar to that of the M. ext. poll. longus. Both are attached to the process of metacarpus I but one on top of the other (the latter under the former), while in most other birds they insert next to one another. The M. flex. carpi ulnaris is very thick and fleshy with

SYSTEMATIC OBSERVATIONS

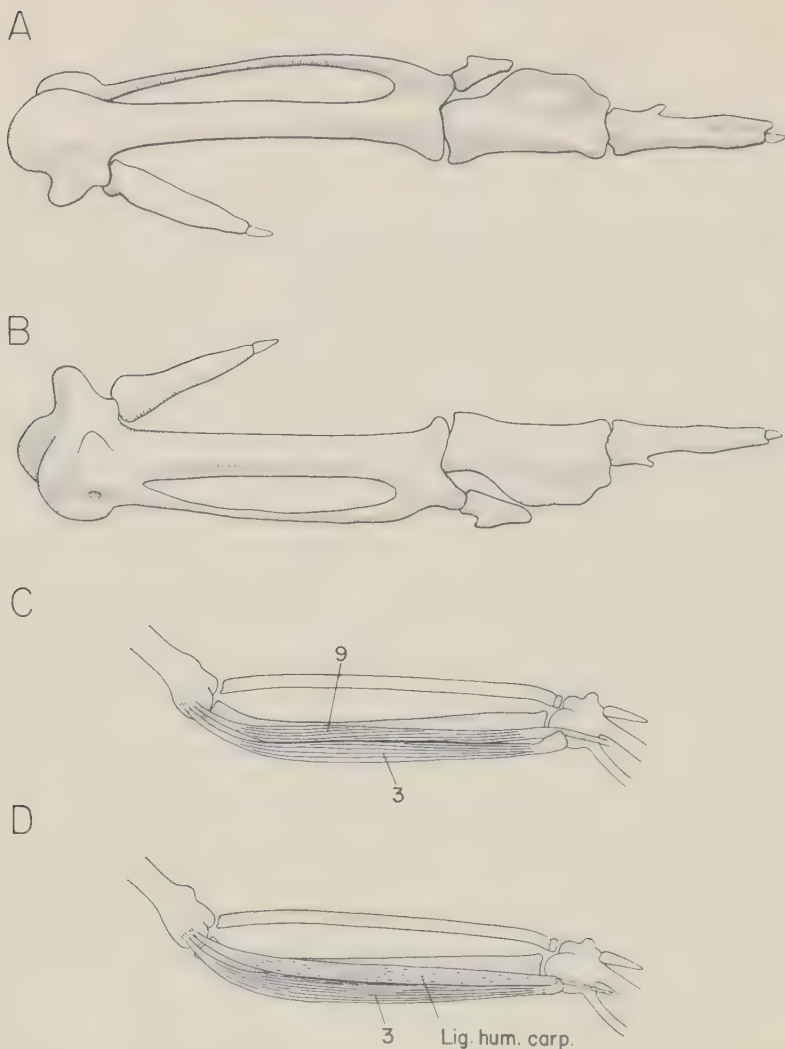


FIG. 1. (A) Dorsum of the manus of *Rhynchotus rufescens*. (B) Venter of the same. (C) Venter of the lower arm of *Tauraco* to show the large M. flex. dig. sublimis and the absence of the Lig. humero-carpale. (D) Venter of the lower arm of *Scolopax* to show the well-developed Lig. humero-carpale and the small M. flex. dig. sublimis, which is hidden under the ligament.

a very short tendon. The M. flex. dig. sublimis is well-developed with its length corresponding to the entire length of the lower arm, while the Lig. humerocarpale is not differentiated (Figs. 1C, 2B, C). The tendon of the M. flex. dig. sublimis inserts on the second phalange of digit II. M. flex. dig. profundus is large; its tendon also inserts on the second phalange of digit II and it can become partly ossified in the segment lying next to metacarpus II. A broad branch of this tendon runs to digit I and extends along the

TINAMIFORMES

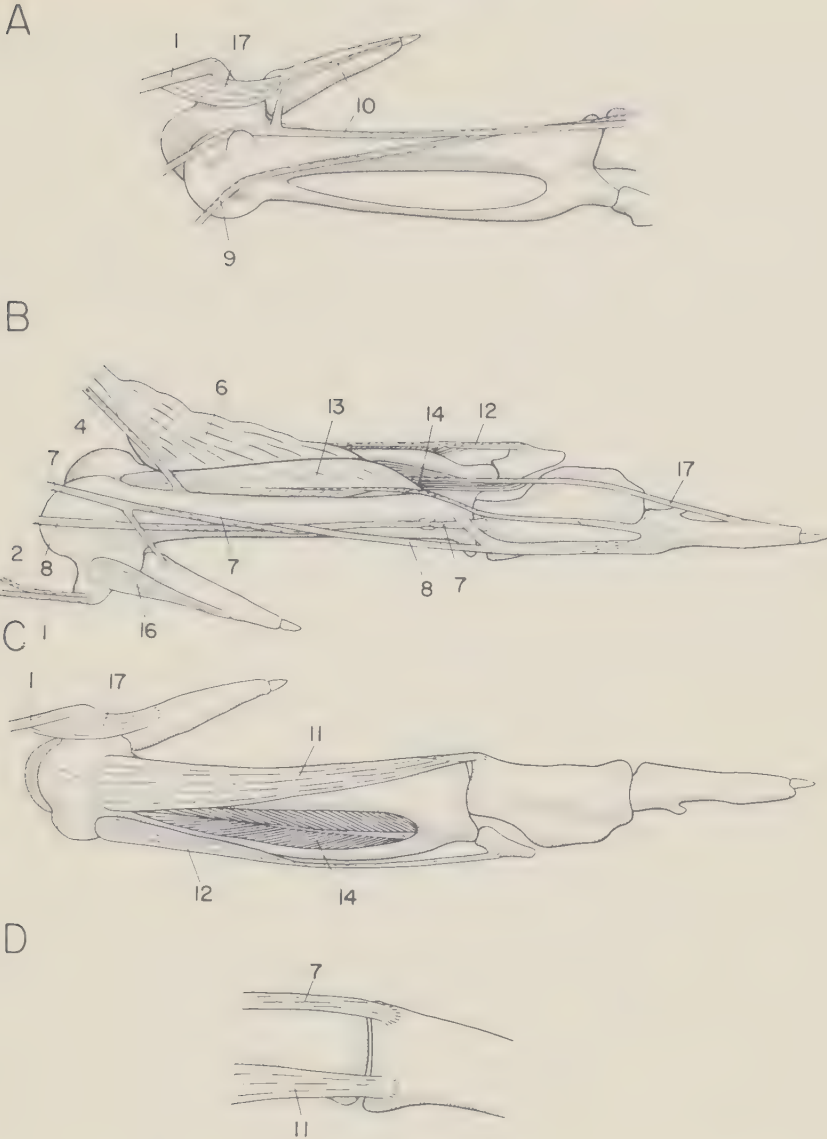


FIG. 2. Manus of *Crypturellus noctivagus*. (A) Venter of the carpometacarpus to show the course of the tendon of the M. flex. dig. profundus. (B) Dorsum of the muscles and tendons of the manus. (C) Venter of the same. (D) Radial view of metacarpus II.

ventral edge of the finger almost up to phalange II (Fig. 2A). The presence of this branch of the tendon of M. flex. dig. profundus seems to indicate that it used to insert on phalanx II of digit I and to function as a flexor for the pollex. In tinamous this function has been lost and the tendon branch to digit I is, therefore, subject to reduction.

In most birds the tendon of the M. flex. dig. sublimis lacks a branch

SYSTEMATIC OBSERVATIONS

going to digit I. Therefore, one can conclude that this peculiar trait in the tinamous is not an evolutionary novelty but an old heritage. Even if this vestigial tendon was well-developed (i.e., inserting onto phalange II of digit I), it would be useless to tinamous, considering their way of life.

This conclusion is supported by ontogenetic data. Geese embryos have a branch of the tendon of the *M. flex. dig. profundus* during the 10th to 13th days of development (Schestakova, 1927), similar to the arrangement characteristic of adult tinamous. A similar arrangement can be found in chicken embryos; however, the branch of the tendon of the *M. flex. dig. profundus* has already disappeared in the newly-hatched young of both the goose and the chicken. One can, therefore, be quite certain that this peculiar feature of tinamous represents an ancestral feature that has been lost in other birds.

The *M. ulni-metacarpalis dorsalis* is massive and reaches approximately to the midpoint of metacarpus III (Fig. 2B). It cannot be separated completely from the *M. flex. dig. III* because fibers of both muscles interweave. The *M. flex. dig. III* is well-developed and partially covers the distal part of the intermetacarpal space (*fissura metacarpi*); however, its proximal border is difficult to follow because it is covered by the *M. ulni-metacarpalis dorsalis* and the two muscles merge somewhat in this region.

The course of the tendon of the *M. ext. dig. communis* is very strange. It lies directly on the surface of the metacarpus II and reaches only to the distal part of a groove to which it inserts; attachment of the tendon is on two bumps at the edges of the groove. In most birds this tendon bends ventrally before its insertion on the first phalange of digit II, so that its insertion occurs on the anterior (radial) side of the finger and closer to the ventral than to the dorsal side. Contraction of the *M. ext. dig. communis*, therefore, causes a supinatory curving of digit II, which was mentioned long ago by Prechtl (1846). From a functional viewpoint, this arrangement in most birds is important because of the possibility of a passive pronatory twisting of digit II caused by the loading of the wing during flight. In tinamous the tendon of the *M. ext. dig. communis* inserts on the dorsal side of the basal phalange of digit II, without the ventral bend characteristic of most birds (Fig. 2D), so that its contraction does not cause any supination, but only an extension of the finger. This is generally characteristic of quadrupeds, including the nonflying ancestors of birds. Therefore, there is no doubt that this aspect of the hand morphology of the tinamous is a primitive feature.

The tendon of the *M. ext. dig. communis* crosses that of the *M. ext. ind. longus*, approximately at the midpoint of metacarpus II. The two tendons twist about one another (Fig. 2B), which serves to hold both tendons in place. In other birds these tendons cross at the proximal end of metacarpus II because the tendon of the *M. ext. dig. communis* lies in a furrow, closely adhering to the bone. The branch of the tendon of this muscle that inserts onto digit I branches off at a very acute angle; the position of this tendon is not fixed by a bony protrusion or a groove (Sy, 1936), but is held in place by surrounding connective tissue.

The tendon of the *M. ext. ind. longus* broadens distally into a wide band

TINAMIFORMES

and inserts on the second phalange of digit II, so that it covers the area of insertion of the *M. inteross. dorsalis*. The *M. abd. indicis* is strongly developed, fleshy along its whole length, and spreads mainly over the anterior (radial) side of metacarpus II, but it also covers the ventral side where it partly covers the intermetacarpal space (Fig. 2C). Its short tendon is attached to digit II without any curve, so that the function of the muscle consists of pure abduction without any rotation (Fig. 2D).

The *M. inteross. dorsalis* is bipinnate and extends to the distal end of the intermetacarpal space. Its tendon curves sharply anteriorly at the distal end of the metacarpus and the proximal end of digit II. At the start of this bend the tendon runs between two bony elevations that hold it in place. Contraction of the *M. inteross. dorsalis* results, therefore, not only in extension of phalange II of digit II, but also in a supinatory rotation of the second finger. As mentioned above, the *M. ext. dig. communis* in the tinamous cannot supinate digit II because of the insertion of its tendon. In these birds supination of the second finger is done by the *M. inteross. dorsalis*, even though it is much weaker than the *M. ext. dig. communis*. Since the explosive take-off of tinamous places a heavy stress on the wings, it is desirable during the downbeat of the wing to have a counteraction to the passive pronation of the wing and of its parts. Yet, the structural arrangements in the tinamous for supination is less effective than that in other birds.

The *M. inteross. palmaris* is also bipinnate and very large. It penetrates through the distal end of the intermetacarpal space to reach the dorsal surface of the metacarpus, extends as far as the proximal part of digit III, and fills exactly the depression of the bone of digit II. Its tendon inserts on the distal part of phalange II of digit II in the usual manner and is supported by the peculiar extension of phalange II (at its proximal end), so that the tendon lies away from the phalange. Of all the muscles of digit I, the *M. extensor pollicis* is the most strongly developed. It not only covers metacarpus I, but also the dorsal and radial sides of digit I almost to the tip of the first phalange. The *M. abd. pollicis* is also large. The *M. add. pollicis* is smaller, while the *M. flex. pollicis* is very small or lacking.

Discussion.—The species of tinamous studied are all very similar in the morphology of their wing. However, the group as a whole differs sharply from all other birds, mainly because of a combination of old and primitive characters, for which reason one would like to put these birds at the beginning of the system of avian classification. This conclusion corresponds completely with earlier investigations of the skull (the palaeognathous palate) of tinamous (see, also, the discussions in Bock, 1963, 1964). One has to mention, however, that these birds, in spite of a great number of primitive characteristics, must have differentiated greatly from the original ancestor of birds because they acquired unique specializations, among others, in the morphology of the wing and in their manner of flight. Tinamous show the same pattern of evolutionary changes that was later undertaken by the gallinaceous birds. But, the tinamous remained far behind the galliforms in their degree of specialization, and this may be regarded as a far from complete attempt to “join the gallinaceous

SYSTEMATIC OBSERVATIONS

birds". At the same time it is clear that the biological way of life ("type") of gallinaceous birds has great advantages and was paralleled by several other groups.

In complete concordance with their ability to take-off rapidly, the tinamous possess very large pectoral muscles (the *M. pectoralis* as well as the *M. supracoracoideus*). The sternum, with its high keel, looks at first sight very chicken-like because the posterior sternal notches (both the lateral and medial) on both sides are very large, leaving little remaining of the breast plate of the sternum. Again, the tinamous are not so specialized as the gallinaceous birds. They lack the indentation at the anterior edge of the keel, in which the filled crop of galliform birds fits, thus facilitating vertical take-off (Stegmann, 1950). They also lack the lateral extension of the sternum (*Processus obliquus* = *pars. lateralis* of the posterolateral process of the sternum), that is characteristic of gallinaceous birds. This difference can be explained by assuming that the ancestors of tinamous possessed only one posterior sternal notch (the medial sternal notch), while the ancestor of the gallinaceous birds had two notches.

In general, one may conclude that the tinamous belong to the most primitive and oldest of avian groups but, on the other hand, they have acquired a high degree of specialization, including features unique for birds. Because of these peculiarities, they should be considered as a side shoot of the avian evolutionary tree that branched off very early, but close to the *Alectoromorphae*.

GRUIFORMES

RALLIDAE

Introduction.—The rails belong to a rather large family of mainly ground-dwelling birds with a world-wide distribution. They live in tropical forests, in swamps, and in the vegetation edging water. Gadow (1891–1893) considered them to be primitive and placed the rails at the bottom of his order Gruiformes. Later the rallids were considered to be more advanced (Peters, 1934; Wetmore, 1960) and were placed higher in the order at a level equal with, or higher than, that of the cranes (*Gruidae*). The peculiarities of the flight apparatus show that Gadow was right.

The wings of the *Rallidae* are small, rounded, and possess relatively weak and soft feathers that are not adapted to carrying heavy loads. In palaearctic and nearctic species the most distal primaries are sabre-shaped and curve backward; when the wing is spread the primaries overlap each other so that the wing appears to be compact (Stegmann, 1952). Rails have 10 primaries, plus a tiny rudimentary 11th. The secondaries are diastataxic.

Species studied.—*Rallus aquaticus*, *R. longirostris*, *Porphyryla parva* (= *P. flavirostris*), *Porphyrio poliocephalus*, *Porzana porzana*, *Porzana paykullii*, *Gallinula chloropus*, *Fulica atra*.

GRUIFORMES

Description.—In all members of the Rallidae the bones of the wing are weak and relatively long and thin (fig. 3A, B). This is very different from the wings of the tinamous. The second phalange of digit I is very well-developed; it is elongate, slightly curved, and has a long pointed claw. The pollex also is very long, being at least half the length of metacarpus II. It is noticeably curved ventrally and less so anteriorly (radially). Metacarpus III is thin, more dorso-ventrally curved than metacarpus II, broadened

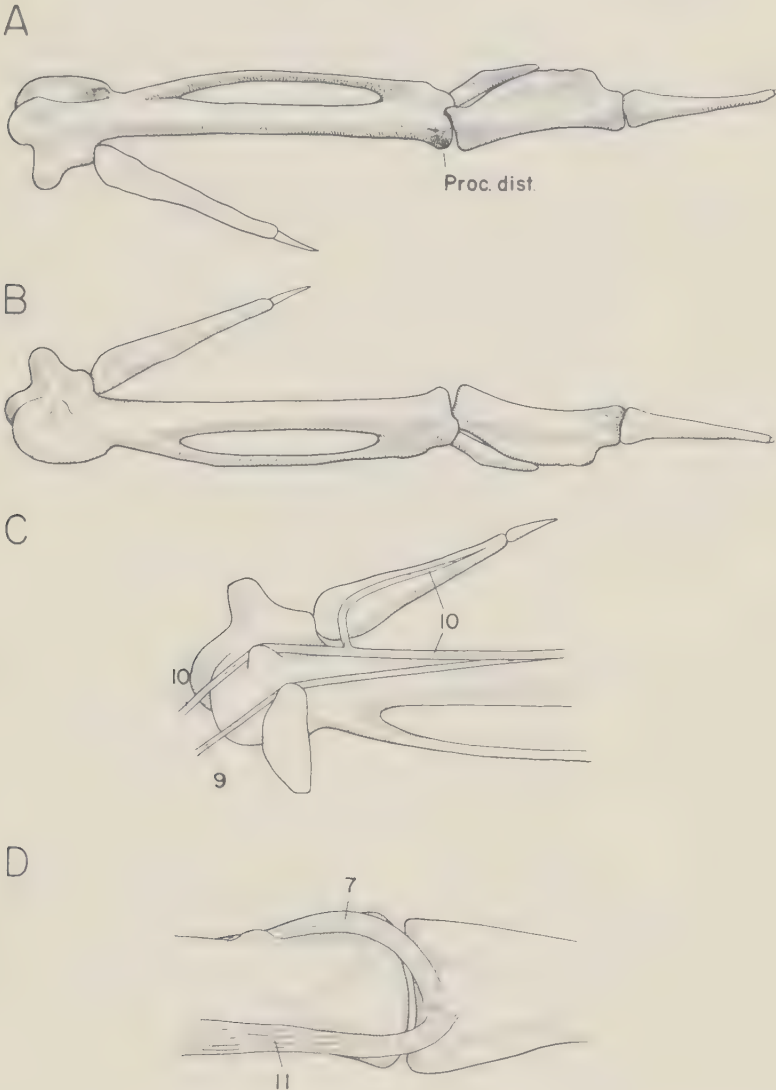


FIG. 3. (A) Dorsum of the manus of *Porzana porzana*. (B) Venter of the same. (C) Venter of the proximal end of the carpometacarpus of *Porphyrula parva* to show the course of the tendon of the M. flex. dig. profundus. (D) Radial view of metacarpus II of *Porzana porzana*.

SYSTEMATIC OBSERVATIONS

proximally, and flattened toward the ulna. Its distal process is well-developed, but not large. The first phalange of digit II is rather narrow and lacks a notch at the proximal end. The second phalange is narrow and hardly shorter than the first. Rails possess a third phalange on digit II, which is, however, small. The third digit is long and narrow, with a slightly developed process.

The wing muscles are conspicuously weak and, accordingly, the tendons are thin (Fig. 4A, B, C). The tendon of the M. ext. metacarpi radialis is as long as the muscle, with a more or less round cross section. The tendon of the M. ext. poll. longus is thin, also is round in cross section, and inserts next to the M. ext. metacarpi radialis; the two tendons join just before their insertion. The M. flex. carpi ulnaris is slender with a rather long tendon. The Lig. humero-carpale is well-developed and forms a broad, strong band. The M. flex. dig. sublimis originates from the inner surface of the L. humero-carpale; it is weak and inserts on the second phalange of digit II. In some rallids, for example in *Porzana*, this tendon does not reach the second phalange, but is attached to a process on the distal end of the first phalange. The M. flex. dig. profundus is one of the strongest muscles of the lower arm. Its tendon inserts at the proximal end of the second phalange of digit II, but a thin vestige of the tendon almost reaches the distal tip of this phalange. The segment of the tendon lying along metacarpus II ossifies, a feature that is seen in its beginning stages in the tinamous. A branch forks off from the tendon of the M. flex. dig. profundus and runs along the ventral side of digit I, almost reaching the second phalange; a peculiarity that is also characteristic of the tinamous. It must be noted that this tendon branch is differentially developed in the various rails. In *Porphyrio* and *Porphyryla* the side branch is as well-developed and extends as far as in the tinamous (Fig. 3C). In *Fulica* the side branch is not so broad as the main tendon, yet it is as well-developed. In *Crex* it is almost as well-developed as in *Fulica*. In *Porzana* it is so thin that it tears easily during preparation. In *Rallus longirostris* (South American specimen) I did not succeed in finding the side branch, while in *R. aquaticus* it was clearly visible as a thin thread-like structure. It is likely that rudiments of this side branch can be found as individual variations in different species of *Rallus*. And it is possible that in other genera of the family the side branch of the tendon of the M. flex. dig. profundus is vestigial and about to disappear. The presence of this side branch, together with the clawed second phalange of digit I, constitutes an apparatus for hooking and is an aid in climbing about in trees, although this capability is as useless to the Rallidae as it is to the Tinamidae. The fact that this tendinous side branch in the Rallidae is vestigial or has even disappeared completely, shows clearly that it is an ancestral character.

The tendon of the M. ext. dig. communis is thin, lies freely on the surface of metacarpus II, and reaches a groove at the distal end of this bone. It inserts on the anterior (radial) surface of the first phalange of digit II, approximately at its midpoint, and therefore, curves sharply before its insertion. Thus, the contraction of the M. ext. dig. communis causes a supinatory rotation of digit II, as is the case in most birds. In this respect,

GRUIFORMES

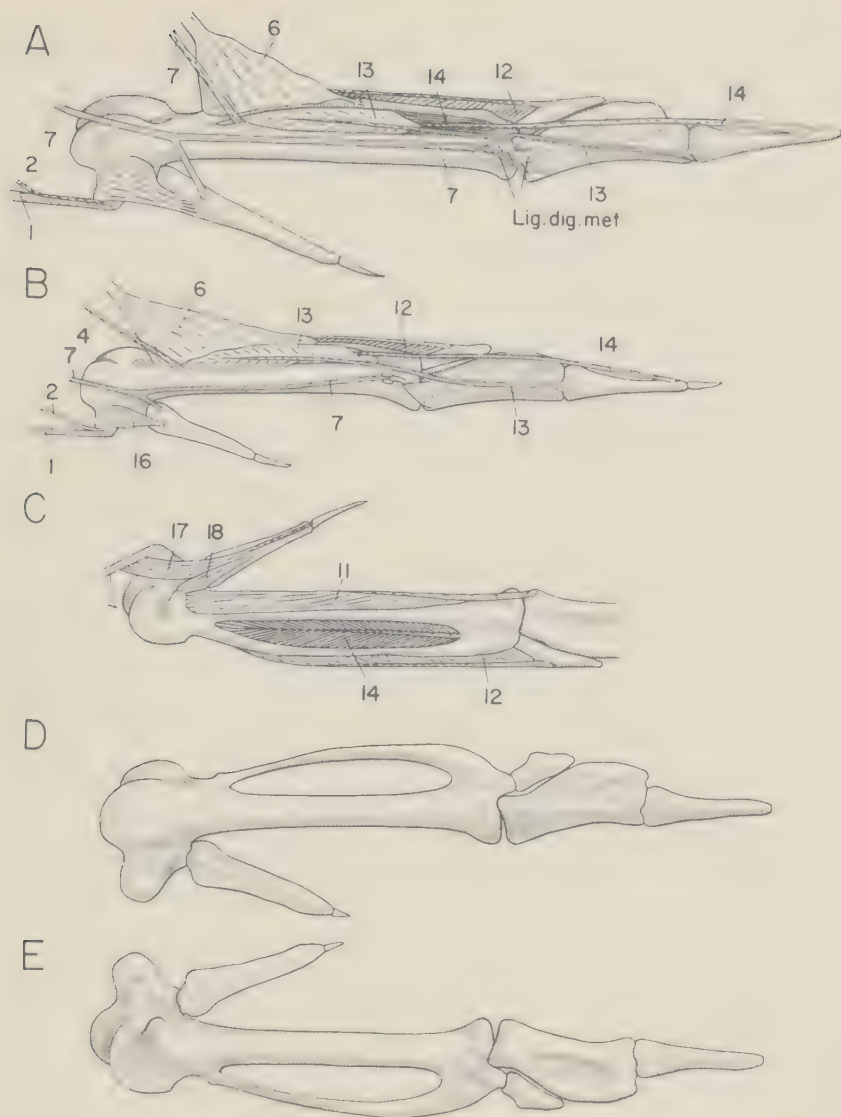


FIG. 4. (A) Dorsum of the manus of *Porzana porzana* to show the musculature. (B) Dorsum of the manus of *Porphyrula parva* to show the musculature. (C) Venter of the carpometacarpus of *Porzana porzana* to show the musculature. (D) Dorsum of the manus of *Macrocephalon maleo*. (E) Venter of the same.

therefore, the Rallidae are more advanced than the Tinamidae (Fig. 3D).

At the start of its curve the tendon of the M. ext. dig. communis has to be fastened to the metacarpus in some way to prevent its slippage when the muscle is in contraction. This is accomplished by a strong ligament that arises from the synovial capsule of the articulation between metacarpus II

SYSTEMATIC OBSERVATIONS

and digit II, which can be named the Lig. digito-metacarpale.¹ This ligament encircles the tendon of the M. ext. dig. communis as a loop (Fig. 4A). The tendon slips easily through the loop, which acts as a pulley, and allows the tendon to curve toward its insertion. Such a pulley for the tendon of the M. ext. dig. communis occurs in many birds. The Rallidae are thus similar to most birds, but differ from the tinamous in which the tendon runs straight to its insertion.

The Lig. digito-metacarpale pulley is, however, not equally well-developed in all Rallidae. In *Porzana*, *Crex* and *Gallinula*, it is well-developed, but in *Rallus*, *Fulica*, and especially in *Porphyrio* and *Porphyrola*, the ligament is less developed. At its curve the tendon is surrounded by strong tissues that attach to the basal end of the finger. Only after these tissues are removed can be seen the small band of fibers looping around the tendon; the loop originates from metacarpus II and runs to the proximal end of the basal phalange of digit II. It seems, therefore, that the Lig. digito-metacarpale is still at the beginning of its evolutionary development in the Rallidae, which suggests that the family is relatively ancient.

The M. ulni-metacarpalis dorsalis is small and weak; its insertion reaches only about one-third of the length of metacarpus III. The unipinnate M. flex. dig. III extends along the posterior edge of metacarpus III as a narrow band, but it is not long because its origin is not at the proximal end of that bone. The two muscles can be easily separated during dissection because they are not grown together. The M. abductor indicis is relatively large, with a short tendon that clearly curves dorsally before its insertion on digit II, so that the muscle not only abducts this finger but also pronates it (Fig. 4C). In the Rallidae this muscle can, therefore, act as an antagonist to the M. ext. dig. communis. The curved portion of the tendon of the M. abd. indicis has to be attached, naturally, and this is achieved with the aid of the distal process of metacarpus II. In the Rallidae this process is positioned closer to the ventral rather than the dorsal side of metacarpus II, and, therefore, can act as a block for the tendon. The distal process also has a groove on its ventral surface through which the tendon of the M. abd. indicis slides. The first phalange of digit II has a process on its anterior (radial) side. The tendon of the M. ext. dig. communis inserts on the dorsal side of this process while that of the M. abd. indicis inserts on its ventral surface. Thus the tendons of these muscles come close to each other, but without actually touching, at their site of insertion.

The bipinnate M. inteross. dorsalis arises from the intermetacarpal space, but its distal end does not reach to the end of the space. Its tendon runs in a straight line to its insertion on the second phalange of digit II, without making the sharp bend characteristic of tinamous. The bipinnate M. inteross.

¹This ligament was usually called the "Lig. antieris ossis metacarpi et I phalanx digiti II", a name also used by Sy (1936). Since this name is needlessly long and because in the present monograph this ligament will be mentioned frequently, it shall be called by the shorter name "Lig. digito-metacarpale".

GRUIFORMES

palmaris also originates from the borders of the intermetacarpal space, but in some species this muscle extends beyond the distal end of the space and can be seen on the dorsal surface of the carpometacarpus. In other species it does not reach the distal end of the intermetacarpal space. Of the muscles which move the pollex, the *M. abductor pollicis* is the largest. From its origin it spreads over the entire basal phalange of digit I, from the ventral edge of the thumb to the radial side, and here lies in contact with the *M. ext. pollicis*, which is moderately large. The *M. flex. pollicis* is always well-developed.

Discussion.—Based on these comparative anatomical studies, one can state that the Rallidae are an old and primitive group which, however, differs sharply from the Tinamidae in a number of important characteristics. In the Rallidae the bones and muscles of the wing are weak, the Lig. humero-carpale is well-developed and the *M. flex. dig. sublimis* is, therefore, small; the tendon of the *M. ext. dig. communis* curves sharply before its insertion and is fastened by a loop of the Lig. digito-metacarpale. The tendon of the *M. abd. indicis* also curves before its insertion, being held in place by sliding along a groove on the distal process of metacarpus II. The *M. flex. dig. III* is distinct from the *M. ulni-metacarpalis*. The *M. flex. pollicis* is well-developed. Finally, the tendons of the *M. ext. metacarpi radialis* and of the *M. ext. poll. longus* differ in form and insertion from those in the tinamous.

Thus, it may be concluded that the Rallidae, even though they are very primitive, cannot be considered to be close relatives of the tinamous. They possess fewer ancestral characters than the latter group and, also, do not show such a high degree of unique specialization that can be readily seen in the evolution of the flying apparatus of the tinamids. The rails probably became ground-living birds a long time ago when they lived in the thickets and underbrush of tropical forests, which presumably was the habitat of the ancestral stock from which rails derived. Whereas the tinamous evolved a quick-starting flight, the ancestral rails specialized in methods of escaping by running and forcing themselves through narrow passages in the thickest undergrowth. Their laterally compressed body is well-adapted for this method of escape. Thus, their flying apparatus remains little specialized.

It is not necessary to assume that the Rallidae and the Tinamidae evolved in the same geographical area. They could have originated in tropical forests on different continents. The different environmental properties of these forests could have selected for diverse flight abilities and wing morphologies of the two groups.

Because there are many flightless species among the Rallidae it is usually assumed that the entire large family is evolving toward flightlessness. To support this view it is argued that rails live in safe habitats, such as swamps, where the ability to fly is unessential (Fürbringer, 1888; Steiner, 1918). It is also frequently said that the relatively weak flying ability of the Rallidae is caused by a reduction of the flying apparatus. Of course, it is not easy

SYSTEMATIC OBSERVATIONS

to decide whether an organ is in the process of evolutionary development or of reduction. In the present case, however, the facts strongly suggest that the rails have never been strong flyers.

It is well-known that reduction of an organ (atrophy) generally leads to disproportional relationships between its constituent parts, since the reduction of all the parts does not occur at the same time or to the same degree. However, the wing morphology of the Rallidae does not fit such a pattern. Although their flying apparatus is weak, it is harmoniously developed. The sternum is small and weak, with a deep notch on each side (similar to that in the tinamous, but not so deep), and the sternal carina is low. The coracoid, clavicle (furcula), and scapula are thin and weak, similar to the bones of the wing. Ligaments connecting the bones are weak. The flight feathers are soft with thin shafts and are lightly attached to the bones. Thus, all parts of the flying apparatus are not geared to high performance. If the gears are weak the motor must not be too powerful. And this is the case in the Rallidae. The main flight muscles (*M. pectoralis*, *M. supracoracoideus*, *M. deltoideus*) are very poorly developed (Stegmann, 1952). Therefore, the flight of these birds is very simple and lacks maneuverability. The small reserve of force in the muscles and weakness of the skeleton of the flying apparatus makes taking-off and landing difficult. But, once airborne, rails are able to fly for quite long distances. This is especially characteristic of the boreal species.

These facts argue against the assumption that the entire family Rallidae has reduced flying ability. It is possible that the Rallidae have remained weak flyers from the time of their origin. The earliest rails might have branched off into a terrestrial habitat (undergrowth of forests) at a time when the main line of birds lived in trees but still flew poorly and still had a primitive flight apparatus. In their subsequent evolution the rails, living in thick undergrowth, did not require any special ability to fly and thus retained the primitive structure and function of their wings. Yet, it must be appreciated that the recent boreal species, even with this primitive flight apparatus, are able to undertake long migrations and, furthermore, that rails have reached and colonized the remotest oceanic islands.

The assumption that the flight apparatus of the Rallidae is primitive is based on the premise that the present radiation of birds stems phylogenetically from a time after they had achieved flight but before flight and the associated morphological adaptations of the wing had been highly perfected.

GALLIFORMES

The gallinaceous birds are a large group with a world-wide distribution. They are generally ground-dwellers living under cover of brush or grass, and are able to take to the air quickly by means of a vertical take-off with high acceleration. Their wings are short and rounded; the flight feathers being extremely strong, hard, and adapted to heavy loading. The longest primaries are narrowed at their tip and are thus modified into very effective

GALLIFORMES

propulsive feathers. Galliforms have 10 primaries and lack a vestigial 11th. The secondaries are eutaxic in most members of this order, but are diastataxic in some megapodes, such as *Macrocephalon* and *Megapodius* (Steiner, 1918). The Galliformes are a well-characterized order. Since the middle of the last century they have been considered to be among the oldest and most primitive birds. They fall into a series of distinct groups which will be discussed separately.

CRACOIDEA

MEGAPODIIDAE

Introduction.—It is generally considered that the megapodes are the most primitive group among the Galliformes. The typical galliform features are not greatly developed in this group. Even though the megapodes are ground-dwelling birds, they still have a foot of the dendrophylic type (anisodactyl) with the posterior toe well-developed and arising from the leg at the same level as the anterior toes. The wing is short and round with strong, hard primaries, but the propulsive feathers are not well-developed. The starting flight (vertical take-off) is not so rapid and highly specialized as in the highly evolved gallinaceous birds. Megapodes live hidden in thickets and high grass; it is very difficult to flush them. As mentioned above, the secondaries in about half the species are diastataxic.

Species studied.—*Macrocephalon maleo*, *Talegalla cuvieri*, *Megapodius nicobariensis*.

Description.—The bones of the wing are strong and massive (Fig. 4D, E). The carpometacarpus is large, but not so large as in the tinamous (Fig. 1A). Digit I has a well-developed second phalange, and digit II has a very small third phalange. Metacarpus II curves noticeably ventrally and slightly radially; it has a distal process. Metacarpus III is thin, but broadens slightly proximally; it curves strongly ventrally. The pollex is very long, not less than half the length of metacarpus II. The basal phalange of digit II is narrower than in the Tinamidae and is notched basally. A thick ridge lies on the dorsal surface of the central broad portion of the first phalange of digit II. To each side of this ridge, that is, on its proximal and its distal sides are strongly depressed areas in which the bony material is so thin that it is translucent (Fig. 4D, E). Many birds possess this structure on the basal phalange of digit II, but in the tinamous it is only slightly developed. The second phalange of digit II is a little shorter than the first and lacks a process on its ulnar side. Digit III is short, broad, and flattened dorsoventrally with a distinct process on its ulnar side similar to that in the Tinamidae.

The muscles of the wing in the Megapodiidae are very thin and long; those of the lower arm, and especially of the hand, are very fleshy (Fig. 5A, B, C). The tendons of the M. ext. metacarpi radialis and of the M. ext. pollicis longus are flat and ribbonlike; the former covers the latter completely. The M. flex. carpi ulnaris is thick and fleshy with a very short

SYSTEMATIC OBSERVATIONS

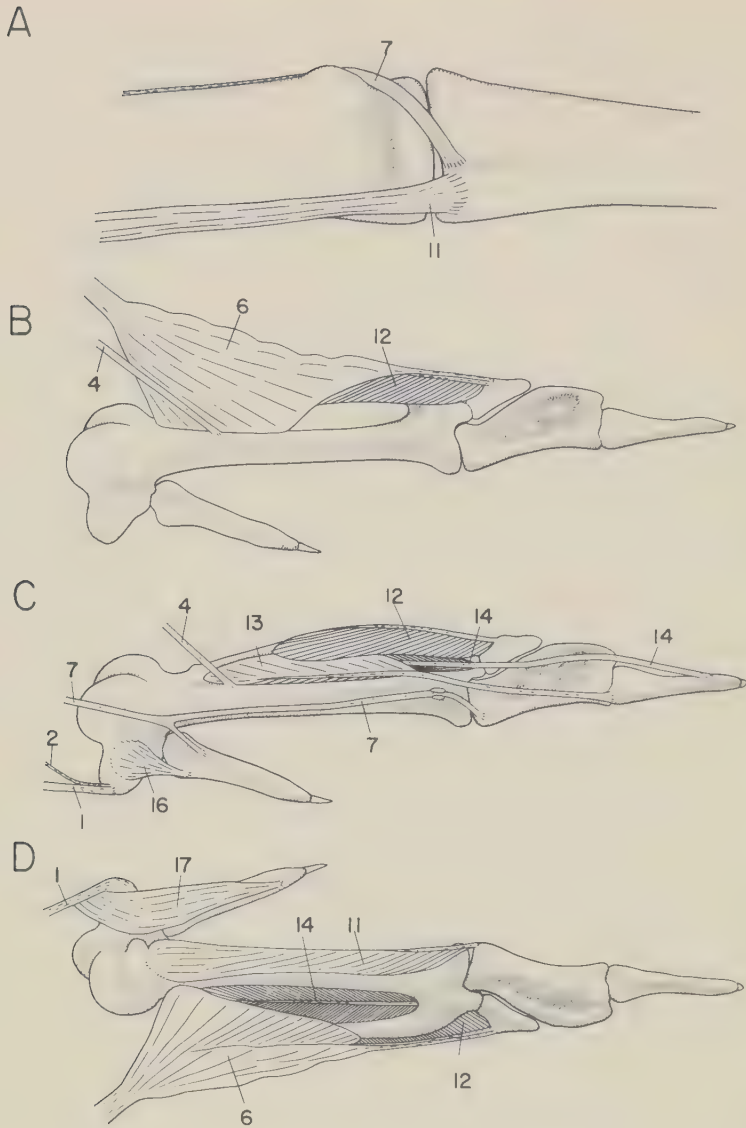


FIG. 5. Manus of *Macrocephalon maleo*. (A) Radial view of metacarpus II. (B) Dorsum of the manus to show the superficial muscles. (C) Dorsum of the manus to show the deeper muscles. (D) Venter of the manus to show the musculature.

tendon. The M. flex. dig. sublimis is very well-developed and presses closely against the former; the Lig. humero-carpale is not developed. The tendon of the M. flex. dig. sublimis inserts on the second phalange of digit II, similar to the insertion of the tendon of the M. flex. dig. profundus. The latter ossifies in the portion lying along metacarpus II. This tendon lacks a side branch that leads to digit I.

GALLIFORMES

The tendon of *M. ext. dig. communis* is thick and strong; it lies in a groove that extends over the greater part of metacarpus II. The tendon curves sharply before its insertion on digit II, so that contraction of this muscle causes a supination of this finger. The *Lig. digito-metacarpale* is lacking; the tendon of the *M. ext. dig. communis* slides over the distal process which lies close to the dorsal side of metacarpus II in these birds. The arrangement for fixation of this tendon at its curve is, therefore, different in principle from that present in the *Rallidae*. The *M. abd. indicis* is large and fleshy. Its tendon runs very straight, without a dorsal curve, so that this muscle only abducts digit II and does not pronate it. This peculiarity is found in the *Tinamidae*, but not in the *Rallidae* (Fig. 5A).

The *M. ulni-metacarpalis dorsalis* is very large and thick (Fig. 5B); it lies along the ulnar side of metacarpus III up to its distal end and inserts via a tendon on the process of digit III. Its contraction causes a curving of the wrist and also an abduction of digits II and III, which results in curving the tip of the wing. The dorsal edge of the *M. ulni-metacarpalis dorsalis* lies against the *M. flex. dig. III* and also partly covers the intermetacarpal space. Its ventral edge overlaps and partly covers the *M. flex. dig. III* (Fig. 5D). The latter muscle is strongly developed and lies partly in the intermetacarpal space, but is in turn covered by the *M. ulni-metacarpalis dorsalis*. The *M. flex. dig. III* is relatively short and does not reach the base of metacarpus III.

The *M. inteross. dorsalis* lies in and extends almost to the distal end of the intermetacarpal space. Its tendon curves radically to reach its site of insertion on the second phalange of digit II (Fig. 5C). The path of the tendon has been described above for the tinamous. Of all the digital muscles, the *M. abductor pollicis* is the best developed. The *M. abductor pollicis* is moderately large, as is the *M. ext. pollicis*, but the *M. flexor pollicis* is lacking or, if present, is very small.

Discussion.—From the above description it can be seen that the *Megapodiidae* lack the most primitive characters of the *Tinamidae*. But, they still retain claws on digits I and II which they possess in common with the *Tinamidae* and the *Rallidae*. A new characteristic is the enormous development of the *M. ulni-metacarpalis dorsalis* which may be regarded as an adaptation to the rapid vertical take-off. The sudden propulsion which occurs in these rapid take-offs acts on the wing tip and may spread the wing too much. A counteracting force must be present to prevent excessive spreading of the wing tip. The *M. ulni-metacarpalis dorsalis*, as the flexor of the wrist, provides the primary force (Stegmann, 1965). In the *Rallidae*, which are not adapted for such a vigorous take-off, this muscle is weak. In the *Tinamidae*, which have for the first time in avian evolution acquired adaptations for a quick, steep take-off, the *M. ulni-metacarpalis dorsalis* is already highly developed but is not so large as in the *Megapodiidae*. Therefore, it can be concluded that the megapodes are more highly specialized than the tinamous in their adaptations for a powerful take-off. On the other hand, the *Tinamidae*

SYSTEMATIC OBSERVATIONS

are more advanced than the Megapodiidae in the external specializations of the wing because they have well-developed propulsive primaries which the megapodes lack.

In general, one can conclude that the Megapodiidae differ strongly from the Rallidae in their wing morphology, but share a number of important characters in common with the Tinamidae.

CRACIDAE

Introduction.—In recent classifications the South American Cracidae have been grouped with the Megapodiidae in a single suborder, in contrast to the remaining, higher galliforms. In fact, the cracids resemble the megapodes in many ways, but in other aspects they are more advanced in their evolution. Like the latter, the cracids have a well-developed hallux that arises from the tarsometatarsus at the same level as the anterior toes. This arrangement is a great advantage because they live in trees and hop with great agility from branch to branch, or run along branches with dancing steps. As tree dwellers they are not dependent on a steep, rapid take-off for escape and they have, therefore, retained broad primaries which are modified into propulsive feathers. The cracids have more or less long tail feathers considering they are forest birds.

Species studied.—*Crax alector*, *C. fasciolata*, *Penelope superciliaris*, *Ortalis vetula*, *O. canicollis*

Description.—The bones of the cracid wing skeleton are about as massive as in the megapodes (Fig. 6A, B). Digit I has a very well-developed second phalange and digit II a vestigial third phalange (Fig. 6). Metacarpus II is strongly curved ventrally and radially. A low elevation is seen at its base; this must be considered as the rudimentary beginning of the muscular tubercle (*Tuberositas muscularis*). In comparison to metacarpus II, metacarpus III is somewhat elongated. Its shape is very different from that in the Megapodiidae; it is broad, twisted and slightly grooved in cross section. The groove at the distal end of metacarpus III faces dorsally, but twists toward the ulnar and finally the ventral plane. At the proximal end the groove again faces the ulnar plane, but this part is separated from the former by a sharp edge. The *M. ulni-metacarpalis dorsalis* attaches to the sharp edge, while the *M. flex. dig. III* attaches to the twisting grooves. The basal phalange of digit II is narrower than in the megapodes, but it is thicker in cross section with a less developed sculpture. Digit III has a very different morphology from that in the megapodes; it is longer and narrower with a slightly developed process.

The cracids are also very similar to the megapodes in the structure of their wing muscles (Fig. 6C, D, E). The tendons of the *M. ext. metacarpi radialis* and of the *M. ext. pollicis longus* are ribbon-like and insert one beneath the other. The *M. flex. dig. sublimis* is large and the *Lig. humero-carpale* is not developed. The tendon of this muscle inserts on the second

GALLIFORMES

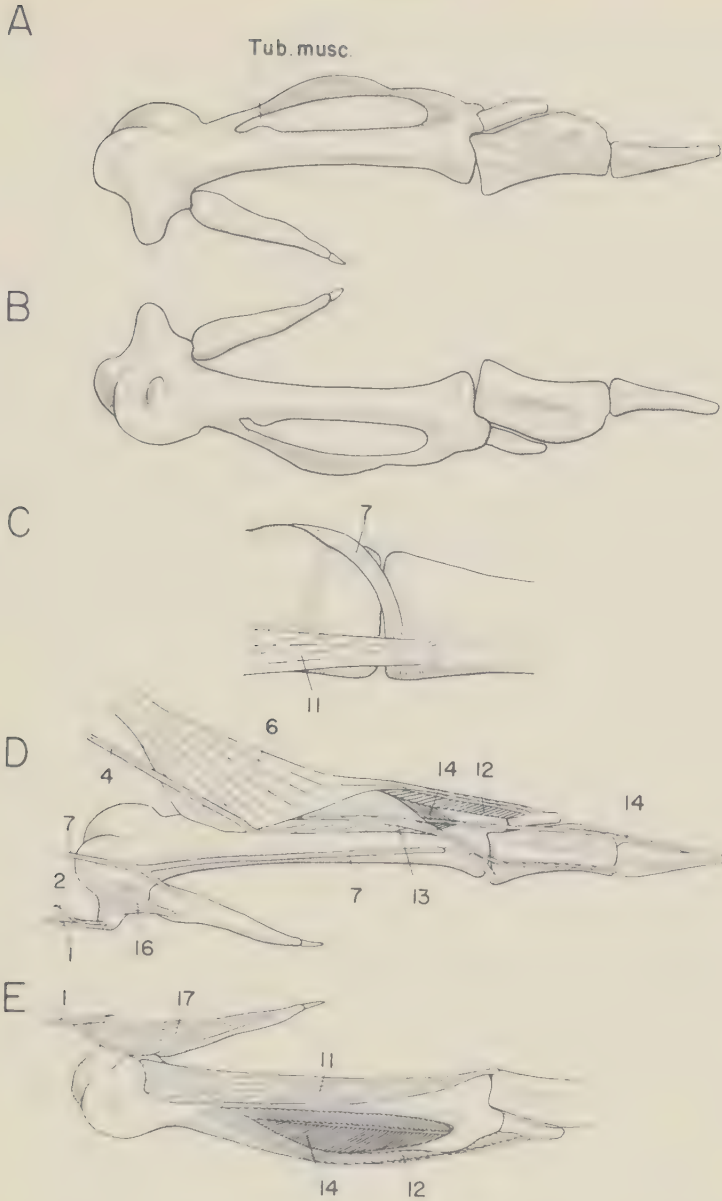


FIG. 6. Manus of *Crax nigra*. (A) Dorsum of the manus. (B) Venter of the same. (C) Radial view of metacarpus II. (D) Dorsum of the manus to show the musculature. (E) Venter of the same.

phalange of digit II, just as does the tendon of the *M. flex. dig. profundus*. The latter tendon ossifies in the segment lying next to the metacarpus; moreover, it has no side branch inserting on digit I. The tendon of the *M. ext. dig. communis* curves sharply before its insertion, sliding over the distal process of metacarpus II. The tendon of the *M. abd. indicis* inserts without

SYSTEMATIC OBSERVATIONS

bending. The *M. ulni-metacarpalis* is very large, partially covers the intermetacarpal space and inserts on digit III via a tendon. The tendon of the *M. inteross. doralis* curves radially at the distal end of metacarpus II. The *M. flex. pollicis* is lacking.

Discussion.—Thus, the Cracidae are very similar to the Megapodiidae in the morphology of the wing. Differences occur mainly in the bones. At this time it is impossible to ascertain the functional significance of these differences. The peculiar form of metacarpus III appears to be a specialization, in contrast to the simpler type found in the Megapodiidae. The beginnings of a muscular tubercle is undoubtedly a progressive character which enhances the usefulness of the *M. flex. metacarpi ulnaris*. This muscle belongs to the flexors of the wrist and better use of its force can aid somewhat the action of the *M. ulni-metacarpalis dorsalis*. It seems that the latter muscle is, indeed, not so strongly developed in the Cracidae as in the Megapodiidae. Therefore, it can be concluded that the Cracidae stand a little higher in their evolutionary development when compared to the Megapodiidae. But the differences between these two groups are not very great. Based upon the comparative anatomy of the wing, one can support completely the conclusion to place the families Megapodiidae and Cracidae in the same suborder (the Cracoidea).

PHASIANOIDEA

This suborder is much larger than the Cracoidea, which consists of the families just discussed. Some workers consider the Phasianoidea to be a superfamily with several families. Others treat the group as a single family with several subfamilies. The relationships expressed in both treatments are exactly the same. I will follow the former arrangement and consider the pheasants, turkeys, and grouse as separate families. The pheasants and their allies are world-wide in distribution and have reached a higher evolutionary position in the order than the two previously discussed groups. Among representatives of the Phasianoidea one finds many characters that indicate high specialization, as well as other characters that are retained ancestral conditions.

PHASIANIDAE

Introduction.—The family Phasianidae has the greatest number of species within the suborder. The characteristics of the skeleton and muscles are quite uniform even though the genera and species are diverse. These birds have evolved to the highest degree of perfection their adaptations for steep, rapid take-offs. The bones of the wing are massive and strong. The remiges are very hard, with stiff shafts that are tightly attached to the wing bones. Propulsive feathers are strongly developed; they diverge at the level of the tips of the upper primary coverts. The flight muscles (*M. pectoralis*, *M. supracoracoideus* and *M. deltoideus*) are very large and strong. A few aberrant genera and species diverge from the great majority of the Galliforms in the

GALLIFORMES

shape of the wing as well as in their type of flight, but the internal morphology of their wings is hardly different from the others.

Species studied.—Odontophorinae: *Odontophorus capueira*, *Lophortyx californica*; Phasianinae: *Gallus gallus*, *Phasianus colchicus*, *Tetraogallus himalayensis*, *Alectoris graeca*, *Perdix perdix*, *Coturnix coturnix*, *Pavo cristatus*.

Description.—The hand bones of the wing in the Phasianidae are stronger and more compact than in the older Galliformes. The intermetacarpal space is broader; hence the whole carpometacarpus appears to be broader (Fig. 7A). Metacarpus II curves less strongly ventrally and radially than in the lower galliforms. The muscular tubercle is well-developed and its tip overlaps the edge of metacarpus III. The distal process is well-developed. Metacarpus III is similar in shape to that found in the Cracidae, but it is much narrower. Digit I has a second phalange somewhat modified into a claw but it is not large. The third phalange of digit II is vestigial. The basal phalange of digit II is broad with a notch at its proximal end; the second phalange is not much shorter than the first. Digit III is about as long as that in the Cracidae, but it has a different shape. It is somewhat laterally compressed and has a well-developed process that is located at the base of the finger, not at its midpoint.

The development of the phasianid flight muscles is, in general, the same as in the Megapodiidae and the Cracidae (Fig. 7B, C). The tendons of the M. ext. metacarpi radialis and of the M. ext. pollicis longus are ribbon-shaped and insert one on top of the other. The M. flex. dig. sublimis is well-developed and the Lig. humero-carpale is not developed. The tendons of these muscles insert on the second phalange of digit II. Likewise, the tendon of the M. flex. dig. profundus inserts on this phalange and ossifies in the portion lying along metacarpus II. The tendon of the M. ext. dig. communis makes a sharp angle ventrally just before its insertion and bends around the distal process (Fig. 7B). The Lig. digito-metacarpalis is lacking. The tendon of the M. abd. indicis runs directly and straight to its insertion, so that this muscle abducts digit II only and does not supinate it (Fig. 7C). The M. ulni-metacarpalis is distinctly smaller. In pheasants this muscle reaches no more than to the basal third of the carpometacarpus, and is only half as heavy as in the Megapodiidae and in the Cracidae. This phenomenon is associated with the presence of a muscular tubercle in the Phasianidae which increases the effective force of the M. flex. carpi ulnaris (Stegmann, 1965). This character places the Phasianidae far above the evolutionary level reached by the galliforms described earlier. It has already been mentioned that in the Cracidae there is the beginning of a muscular tubercle, but this structure was only completely developed where it would be fully effective in the higher galliforms. The M. flex. dig. III is also not as well-developed as in the Megapodiidae and the Cracidae, and it nowhere fills the intermetacarpal space. The tendon of the M. inteross. dorsalis makes a sharper bend at the distal end than is seen in the previously described forms. The M. inteross. palmaris is longer than the intermetacarpal space and reaches the dorsal surface of

SYSTEMATIC OBSERVATIONS

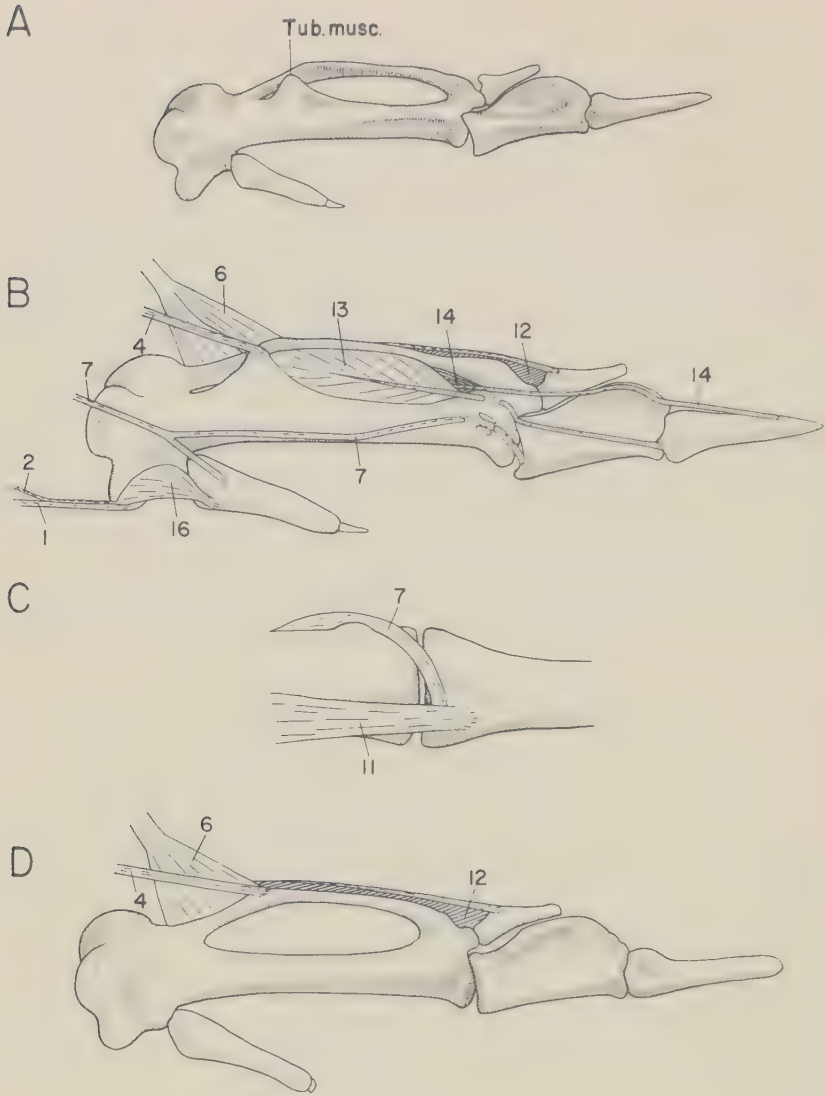


FIG. 7. (A) Dorsum of the manus of *Gallus gallus*. (B) Dorsum of the manus of *Gallus gallus* to show the musculature. (C) Radial view of metacarpus II of *Gallus gallus*. (D) Dorsum of the manus of *Numida meleagris* to show the insertion of the tendon of the M. flex. metacarpi ulnaris.

the metacarpus approximately at the joint of digit III.

These anatomical peculiarities can be found in a similar state in *Gallus*, *Phasianus*, *Perdix*, and *Alectoris*. Moreover, *Tetraogallus* and *Coturnix*, which differ sharply from the other genera in the shape of the wing and in their method of flight, show no remarkable differences from the above mentioned genera in the anatomy of the wing. The species of the subfamily Odonto-

GALLIFORMES

phorinae are not very different from the other phasianids. *Odontophorus capueira* and *Lophortyx californica* are very similar to the phasianines described above. They have a bony projection on the anterior (radial) side of metacarpus II, which fixes the tendon of the M. ext. indicis longus at the point where it crosses the tendon of the M. ext. dig. communis. In addition, the groove on the distal process for the tendon of the M. ext. dig. communis is shallower than in the other members of the Phasianidae studied.

MELEAGRIDIDAE

Introduction.—Fewer peculiarities can be found in the anatomy of the wing in the Meleagrididae than in the families considered earlier.

Species studied.—*Meleagris gallopavo*.

Description.—The carpometacarpal part of the wing in *Meleagris gallopavo* is constructed with a large, strong muscular tubercle exactly as in *Gallus* and *Phasianus*.

NUMIDIDAE

Species studied.—*Numida meleagris*.

Description.—The guinea fowl lack a muscular tubercle on the carpometacarpal part of the wing, a peculiarity that contrasts them sharply with the other galliforms.

Discussion.—One might easily believe that the lack of a tubercle on the carpometacarpus in the guinea fowl represents a primitive condition, because the megapodes also lack a muscular tubercle. However, upon investigation of the wing musculature of the guinea fowl, one learns differently. In these birds the tendon of the M. flex. metacarpi ulnaris is not attached to metacarpus II, but rather to metacarpus III (Fig. 7D). This characteristic of the guinea fowl seems to be very significant, but its origin can easily be explained as follows. The muscular tubercle exists in different birds in extremely different stages of development, ranging from a mere rudiment in the Cracidae to the well-developed process of the Phasianidae and other groups. In the well-developed stage the tip of the muscular tubercle overlaps metacarpus III. Both bones can grow together as, for instance, in the Passeres. In these cases the need for the tubercle is eliminated because the tendon of the M. flex. metacarpi ulnaris almost inserts on metacarpus III because of the close proximity of its insertion on the muscular tubercle to metacarpus III. Such a possibility had been considered before for the Upupidae (Stegmann, 1965). Thus it seems reasonable that the guinea fowl is far advanced over all other members of the Galliformes, because the insertion of the M. flex. metacarpi ulnaris switched from the muscular tubercle to metacarpus III and then the tubercle disappeared.

SYSTEMATIC OBSERVATIONS

TETRAONIDAE

Introduction.—The Tetraonidae differ from the Phasianidae in their way of life as well as in their appearance.

Species studied.—*Lagopus lagopus*, *L. mutus*, *Tetrao urogallus*, *Tetrao tetrix*, *Bonasa bonasia*.

Description.—In the wing morphology of the Tetraonidae there are the following peculiarities, viz., digit I lacks a second phalange, a definite Lig. humero-carpale is present in the lower arm, and the M. flex. sublimis is small. It must be emphasized that these features are not uniform, so that the differences between the Tetraonidae and Phasianidae are blurred. The claw (second phalange) of digit I is very small and dome-shaped in *Perdix*, *Alectoris*, and *Tetraogallus* and is completely lacking in *Crossoptilon*. In these species are found the rudimentary stages in the evolutionary development of the Lig. humero-carpale, which is absent in *Gallus*, *Phasianus*, and *Meleagris*.

Discussion.—In spite of these morphological overlaps, the Tetraonidae form an aberrant group that has evolved from the Phasianidae, a concept that also has been accepted by Peters (1934) and Wetmore (1960).

DISCUSSION

From the above descriptions, it can be appreciated that the Galliformes consist of a number of groups that differ from each other in many ways, but agree in the major features of their morphology. They are birds adapted to a sudden, violent take-off, an ability that has been developed at the expense of several other characteristics of flight. The presence of several aberrant groups can be most easily accounted for by their adaptations to special ways of life. This explanation is strengthened by the observation that the wing morphology in the aberrant groups can be derived from the basic morphology found in the Phasianidae.

Evolution of the rapid, steep take-off was gradual in the Galliformes. The primitive Megapodiidae are ground-dwellers, but their adaptations for a quick take-off is not so strongly developed as in the higher galliforms. It is possible that they have remained at this primitive stage because within their range (Australia, the islands of Polynesia, and a part of Indo-Malaysia) there are few species of ground-dwelling carnivorous mammals.

The Cracidae are arboreal birds; it is not so important for them to have a steep take-off as it is for ground-living galliforms. Therefore, it seems that they have retained a primitive level of adaptation of the wing—a level at approximately the same stage as in the Megapodiidae.

The higher galliforms are again ground-dwelling birds. They are dispersed throughout the world and come into contact with a large number of ground-dwelling carnivores from which there is only one avenue of escape—the rapid vertical take-off. Adaptations for a quick take-off are more advanced

GALLIFORMES

in the higher galliforms than in any other group of birds, including the primitive galliforms.

It is of interest that the great propulsive force developed in quick take-offs has successively led to two different methods of strengthening the ligaments of the wrist. The simplest way was to strengthen the *M. ulni-metacarpalis dorsalis*; this adaptive pathway was taken by the Megapodiidae and the Cracidae. Another, more complicated approach was taken by the higher galliforms, where the need to strengthen the wrist was greater. Here a large muscular tubercle evolved as the site of insertion for the *M. flex. metacarpi ulnaris*. This adaptive pathway was more effective because it (1) increased the use of the *M. flex. metacarpi ulnaris* and (2) provided a greater space for the growth of this muscle.

Evolutionary changes in the sternum can also be easily followed in this order. The sternal keel is higher in the Phasianidae than in the Cracidae. The plate of the sternum still remains in the Cracidae, as well as in the Megapodiidae, even though the four posterior notches are already large. Only in the higher members of the Galliformes does the plate disappear completely since the sternum consists only of a keel and the narrow processes between the large sternal notches. This may be a means of saving weight (Stresemann, 1927-1934) because even though the flight of gallinaceous birds lasts only a short time, there is a heavy load on the flight apparatus.

Thus, within the Galliformes are found a great diversity of specializations from old and primitive to perfected and highly specialized forms. The highly specialized Phasianioidea have the greatest wealth of taxa with 76 genera and 221 species while the Cracoidea have only 18 genera and 64 species (Peters, 1934). One can easily see that the Phasianioidea are still undergoing intensive evolution. Many species are divided into numerous subspecies and there are examples of subspecies that have just reached the species level. A multiplication in the number of species and of different adaptive modifications is in full swing, and one must, therefore, consider these birds as completely modern, in spite of their possession of a number of primitive features.

The adaptive evolution within the Galliformes can be followed easily. They form a special branch of the main phylogenetic tree of birds, at the end of which are the Phasianioidea. Very likely this branch ends blindly. This is because there is no higher evolved group of birds that is closely allied to the Phasianioidea and could be regarded as a further development of this lineage. I shall consider later the phylogenetic relationship of the primitive galliforms to other equally developed groups.

Regarding the relationship of the Galliformes to still older groups, one can say the following. I have discussed the Tinamidae and the Rallidae, two very primitive groups, and have shown that they are, in many respects, very different from each other. An analysis of wing morphology has shown that the Galliformes are closer to the Tinamidae than to the Rallidae. The latter have a well-developed *Lig. humero-carpale*, small tendons of the *M. ext. metacarpi radialis* and of the *M. ext. pollicis longus* which insert next to one another, the tendon of the *M. ext. dig. communis* is fixed at its

SYSTEMATIC OBSERVATIONS

curve with a loop of the Lig. digito-metacarpale, the tendon of the M. abd. indicis curves before its dorsal insertion by gliding over the distal process, and the M. flex. pollicis is well-developed. The Galliformes do not have a well-developed Lig. humero-carpale, but do have a strongly developed M. flex. dig. sublimis. The tendons of the M. ext. metacarpi radialis and the M. ext. pollicis longus are ribbon-like and insert one on top of the other. The tendon of the M. ext. dig. communis slides over the distal process to curve toward its insertion, and there is no Lig. digito-metacarpale. The tendon of the M. abd. indicis does not curve before its insertion, but runs straight. The M. flex. pollicis is lacking. In the Tinamidae all these enumerated characters of the Galliformes are found, except for the curving of the tendon of the M. ext. dig. communis.

As a result of these comparisons one may conclude that the Galliformes agree with the Tinamidae in a series of important features of wing anatomy. Of course the tinamous are far below the gallinaceous birds in the level of their evolution. However, one has the impression that both belong to the same evolutionary lineage, while the Rallidae stand to one side. The rails form the beginning of another line which leads in its further evolution to the Otididae, Gruidae, Charadriidae, and so forth. The reason I have described the Rallidae next to the Tinamidae, and not according to the order of the taxonomic system, is that I wanted to show that although the rails are primitive, they stand far apart from the gallinaceous birds and have very little in common with them.

CUCULIFORMES

The order Cuculiformes contains the families Musophagidae and the Cuculidae, two very different groups, which recently have been placed in different suborders or even orders (Berger, 1960). The relationship of these groups to one another was first recognized by Fürbringer (1888) and Gadow (1891-1893), and subsequently accepted by all workers. However, because they differ from one another in many respects they shall be described separately in order to be able to analyze clearly the phylogenetic situation.

MUSOPHAGIDAE

Introduction.—The Musophagidae are a small group of birds distributed over tropical Africa. All species are aboreal in the fullest sense of the word, inhabiting deep forests and especially gallery forests. They move skillfully in the crowns of trees and in thickets, and rarely come down to the ground. They are plant eaters. They usually do not fly long distances, but have a maneuverable flight which is very well-adapted to their life in thick forests. The wing is broad with a rounded tip, but with poorly developed propulsive feathers. There are 10 primaries, without vestige of an 11th. The secondaries have an eutaxic arrangement.

Species studied.—*Musophaga violacea*, *Tauraco persa*, *T. leucotis*, *Crinifer zonurus*.

CUCULIFORMES

Description.—A biological peculiarity of the Musophagidae should be noted. These birds nest in trees, of course, yet the young leave the nest long before they are able to fly and they climb around on twigs and branches, using their wings continuously. The feathers grow very slowly. According to Pycraft (1904) the body of the small species (*Tauraco macrorhynchus*) is still covered with down at the age of one month but the remiges are growing. Specifically, the inner proximal primaries are almost full-grown while the outer (distal) ones are very small. Retardation of the growth of the outer primaries is probably connected with the fact that young musophagids use their wings for climbing and for this type of locomotion need the claws of digits I and II. At this period the young birds are still able to crawl through the trees with the help of their wings but at the same time are able to undertake gliding flights over short distances, perhaps even flapping a little. The shape of the wing of young musophagids is similar to that of *Archaeopteryx*.

The bones of the hand of the wing in the Musophagidae are short and massive (Fig. 8A, B, C). Metacarpus II is slightly, but not radically, curved ventrally. On its dorsal surface is a deep groove for the tendon of the M. ext. dig. communis. Its distal process is well-developed and lies closer to the dorsum than to the ventral side. Metacarpus III is very broad and flat. Its outer surface is twisted; it is directed ventrally at its proximal end and dorsally at its distal end. At the proximal end there is a distinct edge, similar to that characteristic of the gallinaceous birds, although it is not so strongly developed. In general, metacarpus III most closely resembles that of the Cracidae.

The pollex is approximately half as long as the free part of metacarpus II. The second phalange is rather long, slightly curved, and has a pointed claw. The articulation between the first and second phalanges is well-developed and permits ventral and dorsal movements (flexion and extension). The basal phalange of digit II is massive with smooth surfaces and without the usual surface sculpture. Instead, a groove runs diagonally across the dorsal surface from the proximal-ulnar to distal-radial. The second phalange is noticeably shorter than the first. The third is very small in adult birds and apparently ossifies only incompletely. Digit III is long and has a slightly developed process. In shape it most closely resembles that of the Cracidae.

The muscles of the wing show various peculiarities (Fig. 8C, 9A, B). The M. ext. metacarpi radialis is as long as the M. ext. pollicis longus. The tendons are not ribbon-like, but narrow; they do not insert one on top of the other, and are not coalesced just before their insertion. The M. flex. carpi ulnaris is fleshy with a very short tendon. The M. flex. dig. sublimis is strongly developed; it originates by a strong, short tendon from the distal articular surface of the humerus and is closely appressed to the former muscle. The Lig. humero-carpale is not present as a separate structure as in the Tinamidae and the Galliformes. Berger (1960) describes the Lig. humero-carpale of the touracos as a broad band; this is clearly an error. I have not found such a structure in *Tauraco*, *Musophaga*, or *Crinifer*. In all these genera the M. flex. dig. sublimis is very large and has on its inner side a reinforcement

SYSTEMATIC OBSERVATIONS

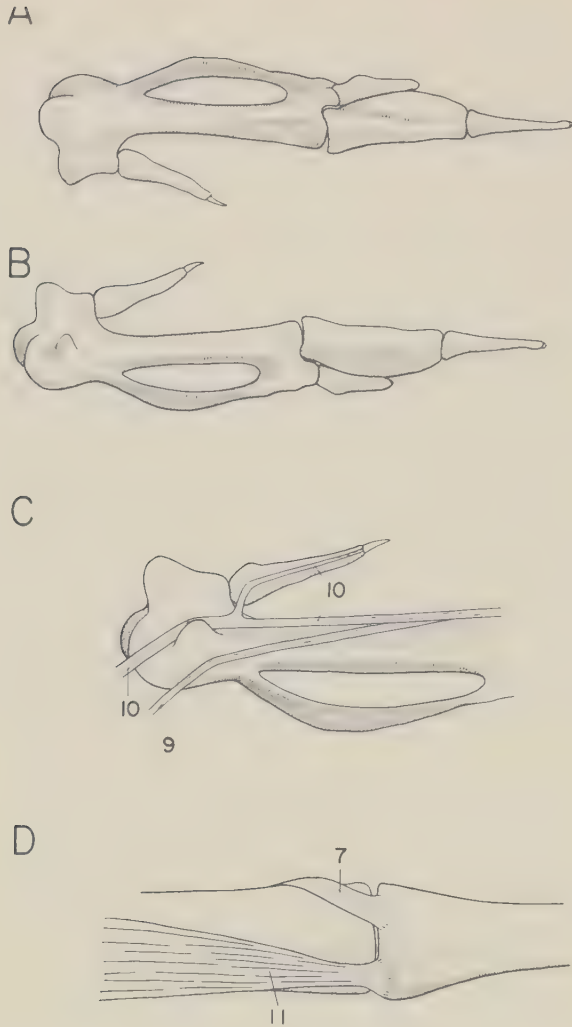


FIG. 8. Manus of *Tauraco persa*. (A) Dorsum of the manus. (B) Venter of the same. (C) Venter of the carpometacarpus to show the course of the tendon of the M. flex. dig. profundus. (D) Radial view of metacarpus II.

of the muscle sheath from which the Lig. humero-carpale has developed as a separate structure in other groups of birds.

The tendon of the M. flex. dig. sublimis inserts on the basal phalange of digit II, which does not occur in lower groups of birds. The tendon of the M. flex. dig. profundus inserts on the third phalange, which is more strongly developed in nonflying young than in adults. A broad branch of this tendon goes to the pollex, running along the ventral side of this digit and inserts on its second phalange (Fig. 8C). Contraction of M. flex. dig.

CUCULIFORMES

profundus thus flexes the claws of digits I and II, which is absolutely essential for climbing in trees with the help of the wings. Thus, for the first time the side branch of the tendon of the *M. flex. dig. profundus* functions fully, but only for the young birds. It can be clearly seen that this character represents a primitive feature, which is eliminated in most birds but remains in some as a vestige. In the young touracos it has retained its full functional ability. It is highly probable that its ontogenetic development in the ancestors of birds took place in a fashion similar to that in the Musophagidae. The altricial and precocial patterns of development later evolved from the musophagid pattern.

The tendon of the *M. ext. dig. communis* extends along metacarpus II in a deep groove. At the proximal end of the metacarpus the tendon is at the anterior (radial) edge. The tendon gradually leaves the radial surface but loops back to it by the distal end. It inserts on the anterior (radial) side of digit II, but closer to its dorsal side than to its midpoint (Figs. 8D, 9A). Thus the *M. ext. dig. communis* supinates digit II less strongly in the Musophagidae than in most other birds, including the Galliformes. The insertion of this tendon is, therefore, approximately intermediate between that found in the Tinamidae and that found in most other birds. The musophagid type of insertion of the *M. ext. dig. communis* is more advanced than in the tinamids, but more primitive than in the gallinaceous birds. The *M. abd. indicis* is very large, even larger than in the Galliformes. Its short, strong tendon inserts without curving dorsally so that the muscle abducts digit II without any pronation. The sites of insertion of the tendons of the *M. abd. indicis* and of the *M. ext. dig. communis* are far apart, almost as is in the tinamous.

The *M. flex. dig. III* consists of two parts. The stronger one originates from metacarpus III at some distance from its proximal end, and partly covers the intermetacarpal space. The second originates from the ventral surface of the outermost base of metacarpus II, and covers ventrally the proximal part of the intermetacarpal space; it sends a long tendon to digit III (Fig. 9B). The *M. ulni-metacarpalis dorsalis* is very large and fleshy, somewhat like that in the Cracidae; it extends to digit III. The extraordinarily strong development of this muscle is very striking and makes it appear similar to that of the primitive Galliformes. The pinnate *M. inteross. dorsalis* almost reaches the distal end of the intermetacarpal space. Its tendon does not curve sharply toward the radial side, as in the Galliformes, but extends diagonally over the basal phalange of digit II, lying in a deep groove on the surface of this phalange. The pinnate *M. inteross. palmaris* is long, reaching the articulation of digit III on the dorsal surface of the carpometacarpus, almost like that in the gallinaceous birds. The *M. abd. pollicis* is smaller, as in the Galliformes, and reaches only to the base of digit I. The *M. ext. pollicis* is rather large and in adults of the genera *Tauraco* and *Crinifer* extends from the rudiment of its tendon to the tip of digit I without reaching the second phalange. It is possible that in young musophagids this tendon inserts on the claw of digit I and extends it.

SYSTEMATIC OBSERVATIONS

Discussion.—In general one may conclude that the Musophagidae show a similarity to the primitive galliforms, especially the Cracidae, in the anatomy of the wing, although there are distinct peculiarities in each group. Because the Musophagidae are more advanced than the Galliformes, one might conclude that the similarities between them are due to convergence. And, because the Cracidae are arboreal as are the Musophagidae, such an assumption seems probable at first glance. But forest birds, restricted to trees, are plentiful, especially among the Coraciiformes and the Passeriformes (for example, the jays), and these have nothing in common with the Musophagidae in the anatomical structure of their wings. There is the reasonable possibility that the similarity in the anatomy of the wing between the Cracidae and the Musophagidae is true ancestral similarity, and hence indicates phylogenetic proximity. The fact that the Musophagidae have remained more primitive in some respects than the Cracidae, in spite of a generally higher evolutionary development, shows that both groups, originating from the same ancestor, have evolved independently over a long time.

CUCULIDAE

Introduction.—The cuckoos, anis, roadrunners, and coucals are a large group of birds of world-wide distribution. Almost all species are restricted to trees, but their habits differ widely, as does their mode of flight. The species of the subfamily Cuculinae are able to make long flights; the largest among them (*Scythrops novaehollandiae*) can even soar. They have rather long pointed wings. The Phaenicophaeinae are true forest birds that are at home in thickets and do not fly far. The wings in these birds are short, broad, and rounded. The Centropodinae resemble the Cuculinae in the shape of the wing, yet these species live in tropical forests and other thick growth near the ground, and they run excellently. Finally, *Geococcyx velox*, a specialized member of the ground cuckoos (the Neomorphinae), runs extremely rapidly in spite of its zygodactylous feet and makes little use of its wings. All cuculids have 10 primaries, without a vestige of the 11th. The secondaries are eutaxic.

Species studied.—*Cuculus canorus*, *C. fugax*, *C. saturatus*, *Clamator glandarius*, *Chrysococcyx cupreus*, *Scythrops novaehollandiae*, *Piaya cayana*, *Crotophaga ani*, *Geococcyx velox*, *Centropus celebensis*, *C. senegalensis*.

Description.—I shall first describe the anatomical characteristics of the wing in the Cuculinae, since representatives of that group were easily available to me, after which I will treat the other forms.

The skeleton of the wing is of similar construction in all species studied (Fig. 9C, D). The upper arm and the lower arm are very markedly shortened, in contrast to the situation in the Musophagidae where the arm bones are of normal length. The manus of the wing is, in contrast to the wing itself, quite long (Fig. 9C, D). Metacarpus II does not curve ventrally or radially. Its distal process is small and located near the dorsal side. Metacarpus III is a little longer than metacarpus II; it is flattened, but is not very broad.

CUCULIFORMES

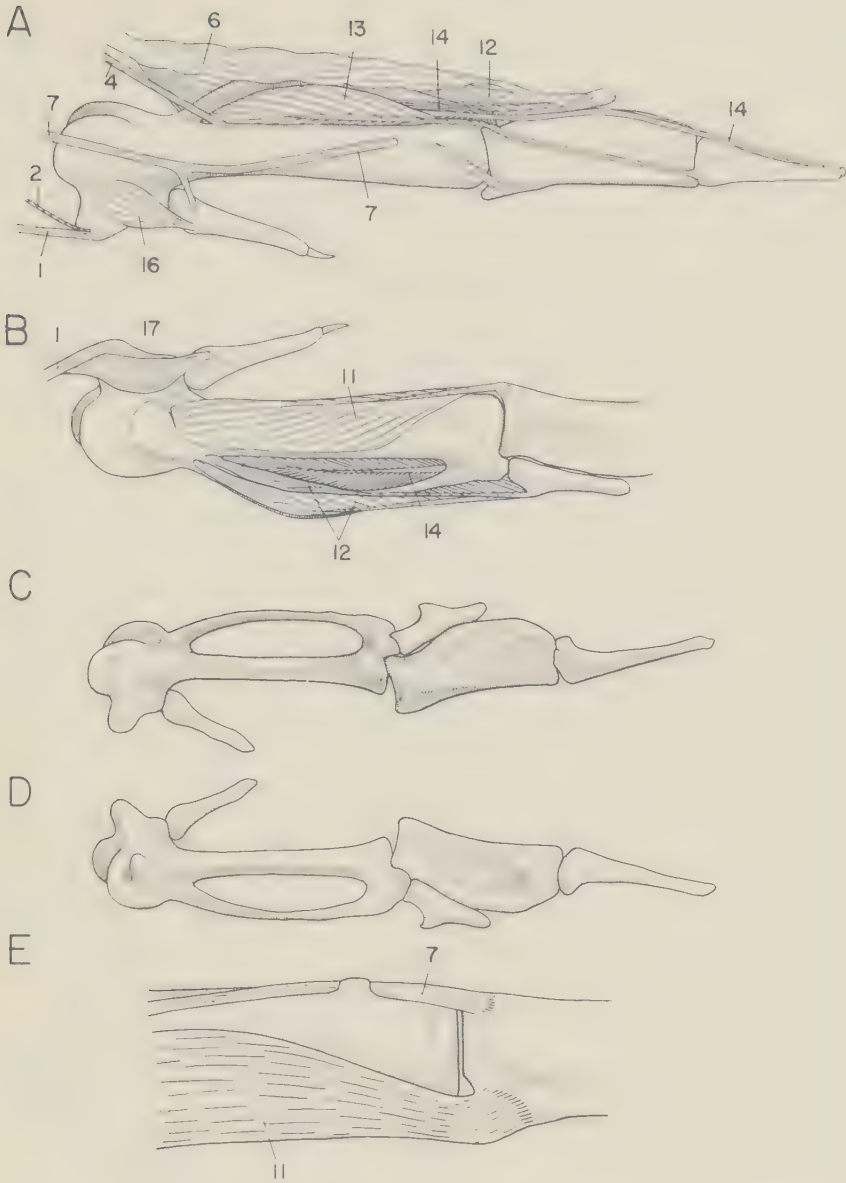


FIG. 9. (A) Dorsum of the manus of *Tauraco persa* to show the musculature. (B) Venter of the same. (C) Dorsum of the manus of *Culculus canorus* (D) Venter of the same. (E) Radial view of metacarpus II of *Culculus canorus*.

and is not twisted, resulting in the flat surface being more or less turned toward the ulna (posteriorly). The intermetacarpal space is broadest at its distal end, giving the cuckoo carpometacarpus a peculiar form. Digit I is about half as long as the free part of metacarpus II, or a little shorter. It lacks even a vestige of a second phalange. This phalange was probably

SYSTEMATIC OBSERVATIONS

lost a short time ago because small corneous formations, which are vestigial claw phalanges, are found on digits I and II in embryonic *Crotophaga ani* shortly before hatching (Stresemann, 1927-34, citing Hartley, 1917). The first phalange of digit II is constructed very differently than in the Musophagidae. It forms a broad plane radially, which is bordered dorsally as well as ventrally by sharp edges. The plate of the basal phalange is rather broad with a well-formed bump at its edge, as well as with a medial elevation. The second phalange has a deep groove on its dorsal side. Digit III is rather long, broad, strongly flattened dorso-ventrally, and has a very large pointed process. The shape of digit III is entirely different from all those previously described.

The skeleton of the carpometacarpus has a very similar morphology in diverse cuckoos. Genera and species differ from one another mainly in the proportions of the skeletal elements. Thus, for example, in *Cuculus fugax* digit II is relatively shorter than that in *C. canorus* or *C. saturatus*, and in *Clamator* the bones of the hand are less massive, with digit II shorter than that in *Cuculus*. But one can always clearly determine from the hand skeleton that the bird is a cuckoo. Even when comparing very small *Chrysococcyx cupreus* with giant *Scythrops novaehollandiae*, one can see immediately the great similarity in the skeleton of the wing.

Some of the representatives of other subfamilies that I have investigated differ from the cuculines much more than do the genera and species of the Cuculinae from each other, just as one would expect. In *Crotophaga ani* and *Piaya cayana*, representatives of the Crotophaginae and Phaenicophaeinae, respectively, the carpometacarpus is shorter and more compact, digit I is longer, and digit II is noticeably shorter than in the Cuculinae. Metacarpus III is considerably broader, somewhat twisted, and resembles that of the Musophagidae. In *Centropus celebensis* and in *C. senegalensis* the bones of the carpometacarpus (Fig. 11B, C) are similar to those in the Phaenicophaeinae but are slightly more compact and shorter. Even in *Geococcyx* the bones of the carpometacarpus are very similar to those of other subfamilies; one can immediately recognize them to be from a cuckoo.

Thus, we see that representatives of the several subgroups of the Cuculidae differ very little in the structure of the skeleton of the carpometacarpus. However, the cuculid type is very characteristic and can be easily differentiated from that of all other birds. It is strange that the Cuculidae are so very different from the Musophagidae in this part of their morphology. Since the time of Föhringer and Gadow we have been accustomed to considering these groups to be closely related. This phylogenetic conclusion is based on a comparative study of a large number of features. To these features may be added the wing bones. It is remarkable and fortuitous that metacarpus III of the short-winged cuckoos is built differently from that in the Cuculinae but in such a way that it is reminiscent of the Musophagidae. Therefore, one may conclude that the short-winged cuckoos are closer to the Musophagidae, or to the ancestor held in common with that family, than are the Cuculinae.

In the structure of the wing musculature the Cuculidae exhibit greater similarity to the Musophagidae (Figs. 9E, 10, 11A, D). In the cuculines the

CUCULIFORMES

muscles of the lower arm are generally large and long with relatively short tendons. The tendons of the M. ext. metacarpi radialis and M. ext. pollicis longus are narrow (not ribbon-shaped) and insert next to one another, just

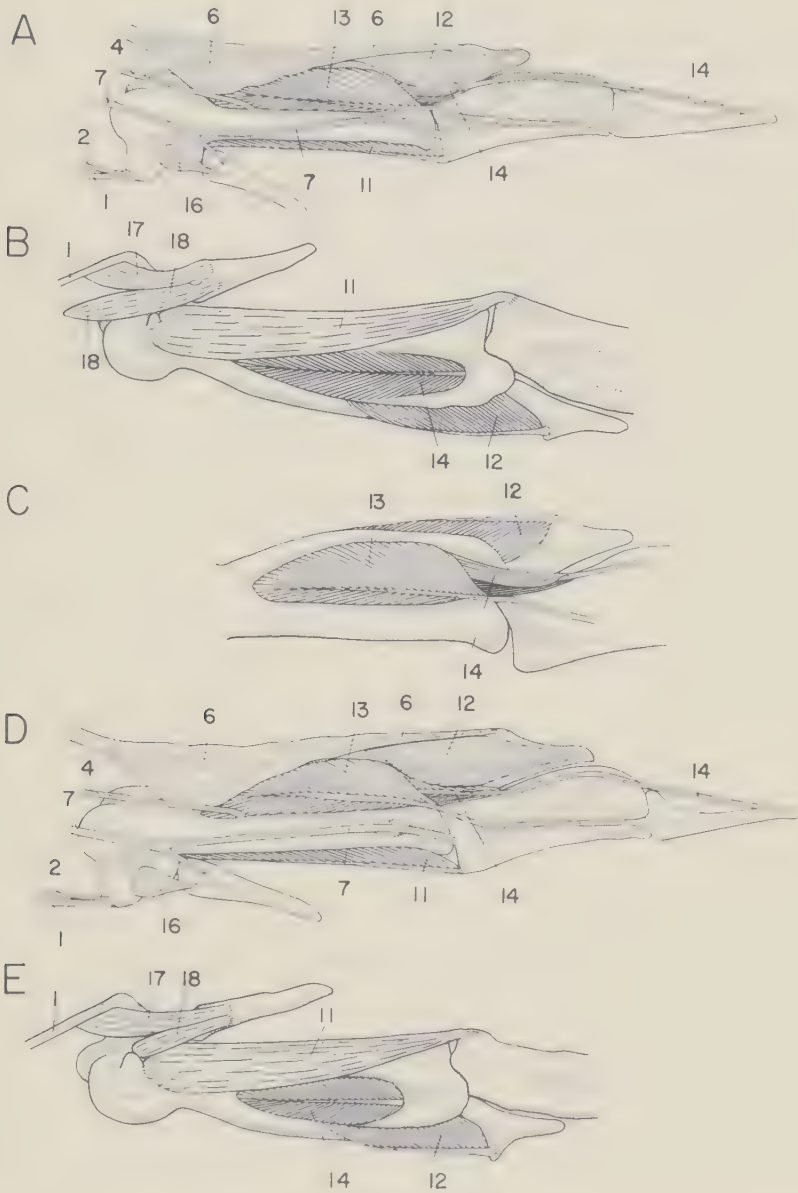


FIG. 10. (A) Dorsum of the manus of *Cuculus canorus* to show the musculature. (B) Venter of the same. (C) Dorsum of the carpometacarpus of *Cuculus canorus* to show the deeper muscles and the characteristic position of the M. inteross. palmaris (the overlying M. flex. dig. III is removed). (D) Dorsum of the manus of *Crotophaga ani* to show the musculature. (E) Venter of the same.

SYSTEMATIC OBSERVATIONS

as in the Musophagidae. The *M. flex. carpi ulnaris* is fleshy with a very short tendon. The *M. flex. dig. sublimis* is well-developed, as in the Musophagidae. The *Lig. humero-carpale* is not present as a distinct structure. The tendon of the *M. flex. dig. sublimis* inserts on the basal phalange of digit II, again similar to that in the Musophagidae. The tendon of the *M. flex. profundus* inserts on the second phalange of digit II. There is no side branch of this tendon going to digit I, a feature that differentiates the Cuculidae from the Musophagidae.

The tendon of the *M. ext. dig. communis* runs in a groove on metacarpus II. It forms a flat arc and inserts on the dorsal edge of the radial surface of the basal phalanx of digit II (Fig. 9D, 10B), similar to the situation in the Tinamidae, i.e., without curving before its insertion. Hence, contraction of the *M. ext. dig. communis* cannot supinate digit II, but can only extend it. This feature of the Cuculidae is extremely primitive and places them at an evolutionary level far below the Galliformes. In the Musophagidae the evolution of the *M. ext. dig. communis* is further advanced since the tendon curves before its insertion, even though this curve is shallower than in most other birds. The *M. abd. indicis* is very large and fleshy; its tendon inserts, without bending, onto digit II, so that it can abduct but not pronate it. This characteristic is common to the Cuculidae, the Musophagidae, the Galliformes, and the Tinamidae.

The *M. flex. dig. III* is short and arises from the middle of metacarpus III. It is, however, thick and fleshy and partially covers the intermetacarpal space; it has a fleshy insertion onto digit III, but leaves the tip of the long process of this digit free. This muscle has two layers. The outer (dorsal) one is as was described; the lower (ventral) one has the usual configuration of this muscle—unipinnate and inserting by a tendon on the process of digit III (Fig. 10B). The *M. ulni-metacarpalis dorsalis* is strongly developed and still larger than that in the Musophagidae. On the dorsal side of the hand it partly covers the intermetacarpal space, as well as the *M. flex. dig. III*. It also inserts on the process of digit III. This muscle has a complicated structure. Several strands of tendons are found on the dorsal surface of the muscle between which the muscle fibers are spread out in several different directions, as is the case in pinnate muscles. The very thick and strong ventral part is also a completely pinnate muscle. This large *M. ulni-metacarpalis dorsalis* has displaced distally the *M. flex. dig. III*, which in turn has displaced radially the *M. inteross. palmaris*. This muscle is very large and extends on the dorsal surface beyond the articulation of digit III, but its ulnar side is bent over by the thick *M. flex. dig. III* (Fig. 10C). This does not occur in other birds. The muscles that control the movement of the pollex are similar to those in the Musophagidae, but in *Cuculus canorus* the *M. flex. pollicis* is not only present but is also larger than in all other birds.

Cuculus canorus and *C. saturatus* can hardly be distinguished from one another in their wing morphology. *Clamator glandarius* is also very similar to these species, but its *M. flex. pollicis* is noticeably smaller. Moreover, giant *Scythrops novaehollandiae* and tiny *Chrysococcyx* are also closely similar

CUCULIFORMES

to the three species just mentioned. The morphology of the wing in the Cuculinae is obviously quite uniform.

In *Crotophaga* the structure of the wing muscles is very similar to that in the Cuculinae; however, its muscles are generally even longer and the tendons shorter. The M. flex. dig. sublimis arises from the humerus by means of a ribbon-shaped tendon, similar to that found in the Musophagidae, rather than from one with a rounded cross-section. This tendon inserts on the basal phalange of digit II. The course of the tendon of the M. flex. profundus is exactly like that in the Cuculinae. The tendon of the M. ext. dig. communis inserts precisely as in the Cuculinae (without curving); it runs along metacarpus II in a straight line, which is a primitive arrangement (Fig. 10D, E, 11A). The M. ulni-metacarpalis dorsalis is fully as strong as in the Cuculinae, and the M. flex. dig. III is just as short and thick. The other muscles do not differ at all from those of the true cuckoos, except that the M. flexor pollicis is considerably smaller. Yet the M. abd. pollicis is large, approximately like that in the Galliformes.

From this comparison it may be concluded that the wing morphology of the *Crotophaga* resembles that of the Cuculinae. The unimportant differences point mainly to the Musophagidae, and especially to the old, primitive features of this group. The wing anatomy of *Piaya cayana* is almost identical to that of *Crotophaga*, which makes its description unnecessary. *Centropus celebensis* and *C. senegalensis* are also very similar to one another (Fig. 11B, C). They are very close to the true cuckoos in wing anatomy but even closer to *Crotophaga* and *Piaya*. They have primitive features especially close to those of the latter.

It was, therefore, completely unexpected to find the anatomy of the wing of *Geococcyx velox* very different from that of other Cuculidae. In general the muscles of the wing of *G. velox* are as developed as those in other cuckoos; the M. flex. dig. sublimis is large without the Lig. humero-carpale and with its tendon attaching to the basal phalanx of digit I, the M. ulni-metacarpalis dorsalis is big and fleshy, etc. The M. abd. pollicis is very large and extends almost to the tip of the pollex, as in the Galliformes. The tendon of the M. flex. dig. profundus is partially ossified in the segment next to metacarpus II, again resembling the Galliformes. However, the course of the tendon of the M. ext. dig. communis in *Geococcyx* is very peculiar for the Cuculidae. It inserts on the anterior (radial) surface of digit II, not far from the site of insertion of the M. abd. indicis (Fig. 11D). Thus the tendon makes a sharp bend ventrally before inserting, so that contraction of the M. ext. dig. communis causes a sharp supination of digit II. The Lig. digito-metacarpale does not exist and the tendon slides over the distal process just like that in the Galliformes.

The wing of *Geococcyx* is rather small, like that in gallinaceous birds, and early ornithologists assumed that the roadrunner was flightless. However, the tendon of the M. ext. dig. communis, which curves strongly before its insertion, is very unusual for the Cuculidae and suggests strong use of the wing. The functional consequences of this arrangement may be demanded

SYSTEMATIC OBSERVATIONS

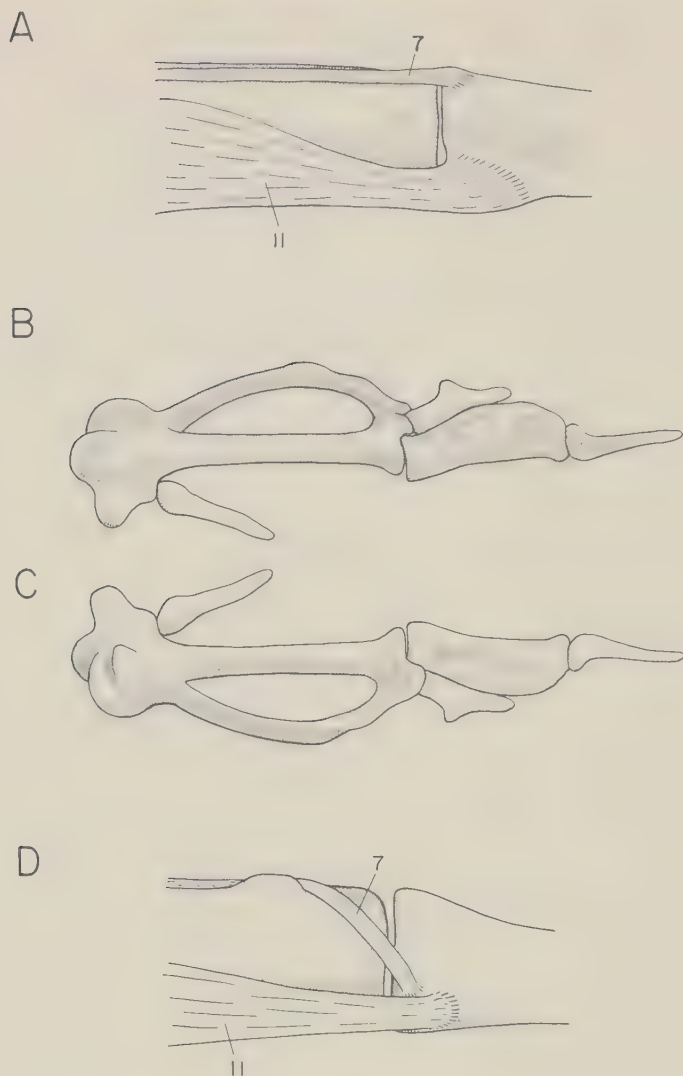


FIG. 11. (A) Radial view of metacarpus II of *Crotophaga ani*. (B) Dorsum of the manus of *Centropus celebensis*. (C) Venter of the same. (D) Radial view of metacarpus II of *Geococcyx velox*.

by a steep take-off, which may be very important for a ground-dwelling bird, living in thickets. Indeed, Bent (1940) notes that *Geococcyx* uses its wings frequently. It often jumps up, flies over thickets, and even catches larger flying insects while coming up from the ground.

Discussion.—With the exception of aberrant *Geococcyx*, the Cuculidae are a very uniform group in their wing morphology. The small differences existing between them show rather clearly that the round-winged forest forms

CUCULIFORMES

are the original ones and have inhabited the tropics for a long time. The Cuculinae subsequently evolved from this basal cuckoo stock. When members of the true cuckoos became able to fly long distances they invaded extra-tropical areas as far as the border of the Arctic. The well-developed and unique specialization of the wing in the Cuculidae (i.e., the maximum development of the *M. ulni-metacarpalis dorsalis*) permits the assumption that the cuckoos represent a terminal branch in avian evolution and are not an ancestral group for other, more highly evolved, birds.

The phylogenetic relationships of the cuckoos to the Musophagidae has been mentioned above. However, it must be emphasized that this affinity, although clear, is not very close. At first examination the wing skeleton of these birds appears to be very different. Only upon closer scrutiny does one discover similarities in some points. These indicate that the more primitive Phaenicophaeinae and Centropodinae have clearer affinities with the Musophagidae than do the more highly organized and more uniquely specialized Cuculinae. In the wing musculature a clear-cut similarity exists between the Musophagidae and the Cuculidae, yet even with these features the relationship between them is not simple. In their morphology the Cuculidae, as well as the Musophagidae, in many respects display further evolutionary advances in the structures found in the Galliformes. The Cuculidae are most advanced in the evolution of the *M. ulni-metacarpalis dorsalis*, while the Musophagidae have remained somewhat primitive in this feature. The absence of the claw on the pollex and on digit II, as well as the lack of the tendon branch leading to digit I must be regarded as progressive characteristics of the Cuculidae, in contrast to the Musophagidae. But, in the insertion of the tendon of the *M. ext. dig. communis* the Cuculidae are even more primitive than the Galliformes.

Based on these comparisons, one may conclude that the Musophagidae and the Cuculidae have descended from the same common ancestor, but have evolved independently for a long time.

One can also conclude from the data presented that the Cuculidae and the Musophagidae are under no circumstances direct descendants of the Galliformes. Although the Cuculiformes resemble primitive Galliformes in their wing anatomy, one finds in the cuckoos some very old characters that have disappeared from the Galliformes. From this one can see that the Galliformes and Cuculidae, although descending from a common ancestor, have further evolved independently and in parallel, and finally formed two end branches in the system.

The question of how the Musophagidae and the Cuculidae should be evaluated does not seem to be too difficult. Even though these groups differ markedly they are more closely related to each other than to any other group of birds, forming a higher level group which may be considered as an order. If one places the Cuculidae and the Musophagidae into separate orders (as does Berger, 1960), one would not take into account their mutual relationships according to our knowledge of their characteristics, including the wing morphology. One must remember, hereby, the excellent advice

SYSTEMATIC OBSERVATIONS

of Max Fürbringer: "Joining, which means to connect correctly, is more difficult than dividing" ("Verbinden, das heisst in der richtigen Weise vereinigen, is mehr als Trennen.").

OPISTHOCOMIFORMES

Introduction.—The order Opisthocomiformes contains a unique species, *Opisthocomus hoatzin*, which inhabits tropical forests of South America. It lives in trees, moving about skillfully. The crop in the hoatzin has taken over the function of the muscular stomach in the digestion of its vegetative food; it is, thus, very enlarged and lies at the anterior end of the sternum which is displaced backward, leaving little room for the pectoral muscles. *Opisthocomus* is, therefore, not able to fly very far and it flutters from tree to tree. But its wings are by no means underdeveloped. On the contrary, they are rather large with sufficiently stiff feathers to be well adapted for gliding flight. The hoatzin has 10 primaries, with no vestige of the 11th. The secondaries have a eutaxic arrangement.

Species studied.—*Opisthocomus hoatzin*.

Description.—The young of *Opisthocomus* have thick down and leave their tree nest very early. They clamber about the trees very skillfully, using their wings as well as feet to grasp the branches; the claws on digits I and II are very useful to the climbing young. The flight feather grow very slowly and the distal-most primaries (the outer ones) lag in their growth behind the proximal ones. Climbing with the help of the wings requires movements of the forelimb that are fundamentally different from flying. Normally birds use synchronized movements of the wings in flight, although this is not an absolute necessity, but in climbing the wings are usually moved asynchronously.

The wing bones in *Opisthocomus* are of normal lengths and are quite strong (Fig. 12A, B). This is also true for the primaries. Metacarpus II is curved sharply ventrally and radially. Its distal process is small and lies in the middle of the anterior (radial) side of the bone. Metacarpus III is flattened and strongly curved. Its outer surface is twisted so that it is turned dorsally at the distal end and more or less ventrally at the proximal end. This peculiarity also occurs in the Cracidae, the Musophagidae, and in the primitive cuckoos. However, *Opisthocomus* is unique in the sudden narrowing of the metacarpus at a point one-third of the distance from its distal end. After this point, the bone gradually broadens again toward its proximal end. Digit I is about two-thirds of the free length of metacarpus II; it is, therefore, extremely long. In the adult the second phalange is very short and domed, yet the joint between the first and second phalanges is well-developed and structured to permit flexion as well as extension. In young birds the second phalange of digit II is compact and with a broad ulnar plate; it resembles that of the Cracidae and even more so that of the Tinamidae. The second phalange of digit II has an articulation at its distal end for a third phalange. This

OPISTHOCOMIFORMES

terminal phalange is small and domed in adults, but larger and has a claw in young birds. Digit III is broad, strongly flattened dorsally, and possesses a long, pointed process. Its structure is exactly like that in the Cuculidae and very different from the birds described above.

The muscles of the lower arm are thick and fleshy with short tendons

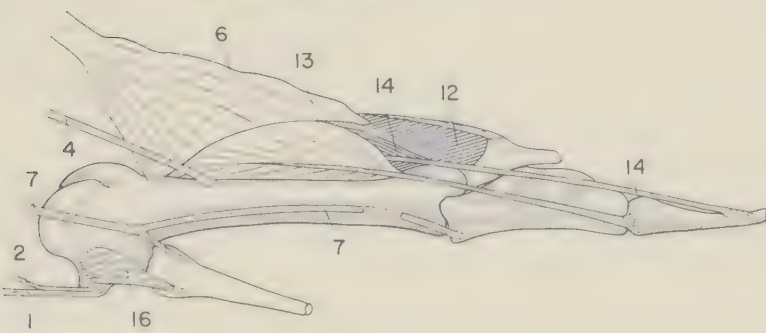
A



B



C



D

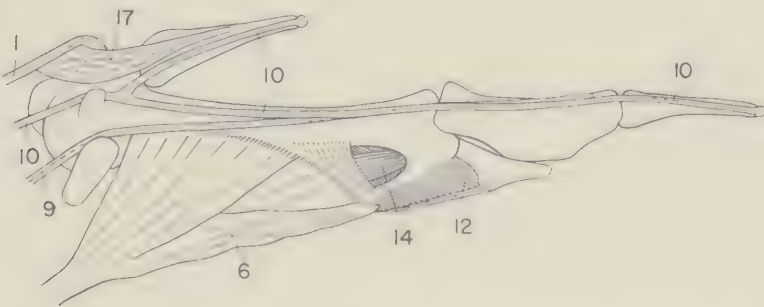


FIG. 12. Manus of *Opisthocomus hoatzin*. (A) Dorsum of the skeleton. (B) Venter of the same. (C) Dorsum of the musculature. (D) Venter of the superficial layer of the musculature.

SYSTEMATIC OBSERVATIONS

(Figs. 12C, D, 13A, B). Tendons of the *M. ext. metacarpi radialis* and the *M. ext. poll. longus* are flat and ribbon-shaped, like those in the Galliformes, but they insert only partly one on top of the other and do not grow together at their insertion, as in the Tinamidae, for instance. The *M. ext. poll. longus* is large and originates from the middle of the lower arm. Its fibers partly interweave with those of the *M. ectepicondylus radialis*. The *M. flex. dig. sublimis* is well-developed and originates via a short thick tendon from the humerus. The Lig. humero-carpale does not exist as a special structure as in the Galliformes. The tendon of insertion of the *M. flex. dig. sublimis* inserts on the second phalange of digit II.

The *M. flex. dig. profundus* is large and long, similar to that in the Galliformes; its tendon inserts onto the third phalange of digit II with a thick side branch of the tendon extending to the pollex, running along its ventral side and inserting on the second phalange (Fig. 12D). Thus, the *M. flex. dig. profundus* flexes the claws (the terminal phalanges) of digits I and II equally and simultaneously. Flexing of these claws serves to grasp branches while clambering through trees, as has already been discussed for the Musophagidae. The tendon of this muscle does not ossify. At the tip of digit II is a blocking device that keeps the claw of this finger in a flexed position, seemingly to relieve the muscles (Banzhaf, 1929) if tension on the claw (contraction of the muscle) should last for some time. Such a blocking device (bony stop) is not present in the Musophagidae.

The tendon of the *M. ext. dig. communis* inserts on the dorsal side of digit II without curving so that it does not supinate this digit as it is extended (Fig. 13A, B). This primitive condition of insertion and action of the *M. ext. dig. communis* occurs in the Tinamidae and the Cuculidae, while the gallinaceous birds are considerably more advanced in this feature.

The *M. flex. dig. III* is short and thick. It originates at the middle of metacarpus III, but does not cover any part of the intermetacarpal space. The *M. ulni-metacarpalis dorsalis* is enormously developed, stronger than in the primitive Galliformes. It covers most of the intermetacarpal space ventrally and is attached to a broad aponeurosis that bridges the distal part of the intermetacarpal space (Fig. 12C, D). On the dorsal side of the manus this muscle also partially covers the intermetacarpal space and the origins of the *M. flex. dig. III* (Fig. 12C, D). At this point it is difficult to separate the several muscles because their fibers intermesh, just as the Tinamidae. The structure of the *M. ulni-metacarpalis dorsalis* is peculiar, yet of the same type as is found in the primitive Galliformes and Cuculidae, being most similar to that in the latter group. The *M. abd. indicis* is large and fleshy; its tendon inserts without curving so that digit II can only be abducted, not pronated (Fig. 13B). The *M. inteross. dorsalis* is well-developed, pinnate, and its tendon extends diagonally over the dorsal side of the first phalanx of digit II without curving radially; again this is similar to that in the Cuculiformes and not like that in the Galliformes. The *M. inteross. palmaris* is large and extends along the dorsal side of the carpometacarpus, but does not reach the articulation of digit III. This muscle has two layers. The inner

OPISTHOCOMIFORMES

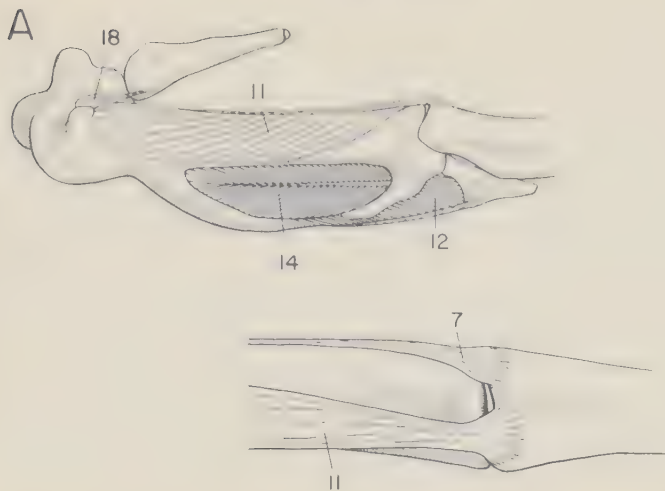


FIG. 13. Manus of *Opisthocomus hoatzin*. (A) Venter of the deeper layer of the musculature. (B) Radial view of metacarpus II.

(dorsal) one is pinnate, as usual; the outer (ventral) one consists of parallel fibers (directed along the length of the muscle) which form a rather narrow ribbon that does not occupy the entire width of the intermetacarpal space (Fig. 12D). This muscle originates from the same aponeurosis to which the *M. ulni-metacarpalis dorsalis* is attached. The *M. ext. pollicis* is large and its tendon reaches the base of the second phalange of the pollex, thus probably being able to extend the phalange. The *M. abd. pollicis*, as well as the *M. add. pollicis*, is normally developed, but the *M. flex. pollicis* could be found as a tiny vestige in only one of the five specimens dissected; in the others it was absent, as is characteristic for the *Tinamidae*, the *Galliformes*, and the *Musophagidae*.

Discussion.—It is obvious from the above description that *Opisthocomus* cannot be placed among the *Galliformes*, even if given a very isolated position among them as is done currently. A series of morphological characters in the hoatzin differentiates it sharply from the *Galliformes*, but brings it closer to other groups. If one proceeds purely statistically, the following conclusions are reached. Of the 17 morphological features described in the manus of *Opisthocomus*, five are shared with the *Cuculidae*, three with the *Musophagidae*, three with the *Galliformes*, one with the *Galliformes* and *Musophagidae*, one with the *Musophagidae* and the *Cuculidae*, and four with the *Galliformes*, the *Musophagidae*, and the *Cuculidae*. Thus, *Opisthocomus* shares the greatest number of characters in common with the *Cuculidae*. It has the same number of characters in common with the *Galliformes* and the *Musophagidae*, namely three. But if one considers that the *Musophagidae* and the *Cuculidae* belong to the same order, the number of similar features they share with *Opisthocomus* is more than twice the number of similar features shared by *Opisthocomus*

SYSTEMATIC OBSERVATIONS

and the Galliformes. Therefore, *Opisthocomus* should be placed in the Cuculiformes.

However, if one weighs the differing degrees of importance of these characteristics (their different taxonomic value), one comes to a different conclusion. For instance, all of these groups have in common the enormous development of the M. ulni-metacarpalis dorsalis, which separates them from all other birds. However, from the evolution of this character we can draw the following important conclusions. In the primitive Galliformes adaptation for a rapid take-off leads to the strong development of the M. ulni-metacarpalis dorsalis. In the higher Galliformes this muscle has degenerated because the evolution of the muscular tubercle leads to greater efficiency of the M. flex. metacarpi ulnaris, which supplanted the former muscle. Other related groups that are all arboreal retain the strong development of the M. ulni-metacarpalis dorsalis, which they had inherited from their ancestors. The fact that this muscle has been retained in *Opisthocomus* in its strongest development shows that the ancestors of this bird were able to fly actively. Because this muscle, except for its strong development, is structured similarly in all these groups, one can assume that their evolution did not occur in parallel, but that they are descended from a common ancestor.

Another morphological feature, the method of insertion of the tendon of the M. ext. dig. communis, also permits several conclusions. In *Opisthocomus* and in the Cuculidae it remains very primitive, while in the Galliformes it is greatly advanced because of its ability to rotate and supinate digit II. However, because the Galliformes, in general, are more primitive than the Cuculidae, one has to conclude that these groups and *Opisthocomus* became separated before the Galliformes acquired the present highly developed manner of insertion of the aforementioned tendon. It is possible that the Galliformes acquired this particular morphological character because of their adaptation to a rapid take-off, while the Cuculidae and *Opisthocomus*, as arboreal birds, could have retained the old, primitive type of insertion. The Musophagidae have evolved in this respect further, but without reaching the advanced stage of the Galliformes. It is probable that they are better able to execute the "hover flight" ("Rüttelflüge") than can the Cuculidae and *Opisthocomus*.

The presence of claws on digits I and II, as well as the branch of the tendon of the M. flex. dig. profundus which goes to the terminal phalange of the pollex, are also very primitive characters. In the Tinamidae the entire set of features was retained, even though somewhat degenerated. It has no functional meaning and has been acquired from its ancestors as a phylogenetic inheritance. The Galliformes still have claw phalanges on digits I and II, although only small ones, but the branch of the tendon of the M. flex. dig. profundus, which leads to the pollex, has disappeared. Because the Galliformes have evolved farther than the Tinamidae, it is to be expected that they should have a greater reduction of the apparatus for climbing with the help of the wings. The unique ontogenetic development of the Musophagidae and of *Opisthocomus* permits this apparatus to remain intact and retain its function. The immediate ancestors of these birds were arboreal and the

GRUIFORMES

earliest birds also lived in trees. Therefore, it seems plausible that their ontogenetic development occurred in the same way as it does today in *Opisthocomus* (and in the Musophagidae). The morphological character which is associated with this ontogenetic development is, therefore, an evolutionarily primary character and did not develop secondarily. It also would be against all logic to assume that the side branch of the tendon of the M. flex. dig. profundus, which leads to the pollex, could have evolved again in a similar way after it had been lost, especially since this morphological character has a functional advantage only after it is fully developed.

Therefore, it is clear that the peculiarity of the ontogenetic development, as well as the morphological characters associated with it, ally *Opisthocomus* close to the Musophagidae. But in other respects it shows similarities to the Cuculidae, the Galliformes, and finally also to the Tinamidae. Thus, the only remaining possibility is to consider *Opisthocomus* as the sole representative of its own order and to rank it next to the Galliformes, but lower than the Cuculiformes. All of these groups have different morphological features that interrelate them and that contrast them with all other birds. Therefore, one can combine them into a single higher group, the superorder Alectoromorphae. The Tinamiformes, which as "Palaeognathae" have to rank much below all flying birds, also belong to this group according to the morphology of their wing. But since they are very primitive in this respect they should be placed at the lowest level of the classification of the Alectoromorphae.

In many respects the Rallidae are different from the Alectoromorphae, as they are constituted here. They are also primitive, but they form the beginning of another series of groups which I propose to name the Charadriomorphae.

GRUIFORMES

TURNICIDAE

Introduction.—The hemipodes, or buttonquail, are a small group of quail-like birds that inhabit southern Europe, southern Asia, Africa, and Australia. They are ground birds in the fullest sense of the word. They are not able to perch on branches and twigs, and lead a hidden life in high grass and brush. They do not occur in swampy habitats. The wing of the Turnicidae is short, but narrower than in the Galliformes. The wing tip is closed with no gaps between the primaries since the outermost primaries are bent backward in a curve. There are 10 primaries, with a tiny vestige of the 11th. *Turnix* and *Ortyxelos* are eutaxic; *Pedionomus* is diastataxic.

Species studied.—*Turnix tanki*.

Description.—The bones of the wing are short in the Turnicidae, but not nearly so compact and strong as in the Galliformes. The manus is longer and narrower (Fig. 14A, B). Metacarpus II curves ventrally and radially.

SYSTEMATIC OBSERVATIONS

but only weakly. A groove for the tendon of the *M. ext. dig. communis* is present only at the distal end of the carpometacarpus. A small, but quite visible, muscular tubercle is present. The distal process is dorso-ventrally flattened and is curved somewhat ventrally. Metacarpus III is not broad, but is flattened along its entire length and twisted so that its proximal part is directed ventrally and its distal part dorsally. Digit I is rather long, but shorter than half the length of metacarpus II. Its second phalange is very small and vestigial, and appears to ossify incompletely. The basal phalange of digit II is less massive than in the Galliformes, more like that in the Rallidae, and the sculpturing on its upper surface is little-developed. The second phalange of digit II is relatively longer and narrower than in the Galliformes. Digit II is short and dorso-ventrally flattened, but broad and with a large pointed process almost like that in the Cuculidae.

In the structure of its wing musculature *Turnix* resembles the Rallidae more than the Galliformes (Fig. 14C, D, E). The muscles of the lower arm are shorter than those in the Galliformes but with longer tendons and, therefore almost like those in the Rallidae. The tendons of the *M. ext. metacarpi radialis* and of the *M. ext. poll. longus* are narrow, not ribbon-like, and insert next to one another, rather than one on top of the other; they do not grow together just before their insertion. All these characteristics are similar to those in the Rallidae. The Lig. humero-carpale is a well-developed broad ribbon, as in the Rallidae; the weak *M. flex. dig. sublimis* originates from its inner side. The tendon of this muscle inserts on the second phalange of digit II, as does the tendon of the *M. flex. dig. communis*. The latter muscle ossifies in the segment lying next to metacarpus II but does not send a side branch to digit I.

The tendon of the *M. ext. dig. communis* is thin, as in the Rallidae, and inserts very close to the dorsal side of digit II; it makes only a very slight curve before its insertion and, hence, can supinate the digit only weakly (Fig. 14C, E). In this respect *Turnix* is more primitive than the Galliformes and also more so than the Rallidae. The slight bend of this tendon is not held in place by a well-developed Lig. digito-metacarpale, but rather is enclosed entirely by connective tissue that is attached mainly to the base of the finger. If this fibrous connective tissue is removed in thin layers a small number of fibers can be seen that are wound around the tendon and are fastened to the distal end of the carpometacarpus, thus forming the beginning rudiments of the Lig. digito-metacarpale, as has already been described for the Rallidae. The *M. abd. indicis* is strong with a short tendon that makes a sharp dorsal curve before inserting on digit II, thus pronating this finger. It slides over the distal process, which is curved ventrally and lies somewhat over the tendon (Fig. 14E). This is another feature that is basically similar to that in the Rallidae.

The *M. ulni-metacarpalis dorsalis* is fleshy but as small as in the Rallidae. The *M. flex. dig. III* originates from the outer edge of the proximal end of metacarpus II and runs as a narrow muscular band to digit III. The *M. inteross. dorsalis* is pinnate and its tendon curves abruptly at the distal end

GRUIFORMES

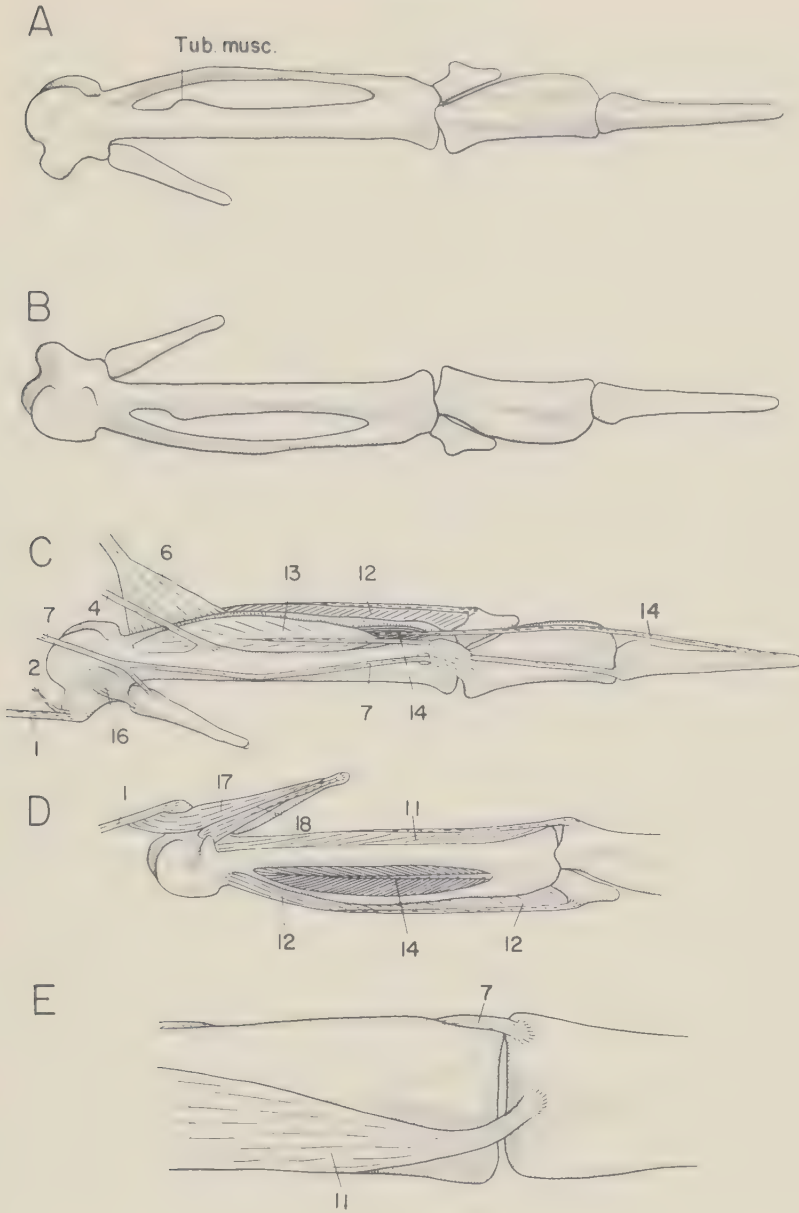


FIG. 14. Manus of *Turnix tanki*. (A) Dorsum of the skeleton. (B) Venter of the same. (C) Dorsum of the musculature. (D) Venter of the same. (E) Radial view of metacarpus II.

of metacarpus II toward the radial side, somewhat like that in the Galliformes. Its curved portion is held in place by the same mass of connective tissue that winds around the tendon of the *M. ext. dig. communis*. The *M. inteross. palmaris* is pinnate and long; it crosses to the dorsal side of the carpometa-

SYSTEMATIC OBSERVATIONS

through the distal end of the intermetacarpal space, but does not reach the articulation of digit III. The set of muscles to the pollex is complete. The *M. abd. pollicis* is very large and reaches almost to the tip of digit I. The *M. flex. pollicis* is normally developed (Fig. 14D).

Discussion.—The above description of the hand skeleton and musculature shows that *Turnix* has little in common with the Galliformes, but rather is much more similar to the Rallidae. In one respect it is more primitive than the Rallidae, viz., in that the tendon of the *M. ext. dig. communis* curves only slightly before its insertion rather than sharply as in the rails and in most other birds. Therefore, this feature must be considered to be very primitive, especially since the curved tendon is bound to the carpometacarpus in a primitive fashion. In general, however, the Turnicidae are evolutionarily more advanced and specialized than the Rallidae. In the buttonquail, the branch of the tendon of *M. flex. dig. profundus* that goes to the pollex is missing, the second phalange of digit I is vestigial or entirely lacking, and a small muscular tubercle is present. The last character suggests that the flight of *Turnix* must be stronger than that in the Rallidae. The *M. ulni-metacarpalis dorsalis* is not large in *Turnix* and from this it may be concluded that the turnicids specialized in a different way than did the Galliformes. In the latter group the *M. ulni-metacarpalis dorsalis* was fully enlarged first and only subsequently did the muscular tubercle appear and enlarge. In *Turnix* specialization started with the evolution of the muscular tubercle, so that the appearance of this feature did not affect the *M. ulni-metacarpalis dorsalis*. Hence, in the Galliformes and in *Turnix* the adaptative evolutionary changes to the same environmental demands (selection force) occurred in different ways. This testifies against the phylogenetic closeness of these groups.

Other aspects in the wing morphology of *Turnix* also indicate that this bird has a stronger flight and is capable of more rapid take-offs than the Rallidae. The bones of the carpometacarpus are stronger and more compact, metacarpus III is broader and offers more area for origin of the *M. flex. dig. III*, and all muscles are larger with more fibers than in the Rallidae.

Field observations confirm the functional assumptions based on the morphological findings. The buttonquail lead secretive lives on the ground and fly up rapidly and steeply at the approach of danger. In this way they resemble the Galliformes more than the Rallidae. Yet, in its morphological structure the wing of *Turnix* is a rallid wing, although the primaries are markedly stiffer than those of the Rallidae and the outermost secondary is shorter (Fig. 15), which reduces the tendency toward severe twisting of the wing during high loading (Stegmann, 1969). In *Pedionomus* the first two secondaries are shortened (Steiner, 1918; Stresemann, 1927-34).

The main flight muscles are noticeably more strongly developed in *Turnix* than in the Rallidae. In the latter the total weight of the *M. pectoralis*, the *M. supracoracoideus*, and the *M. deltoideus* (both sides) amounts to about 11-12% of the bodyweight (Stegmann, 1952) while in *Turnix tanki* these muscles

GRUIFORMES

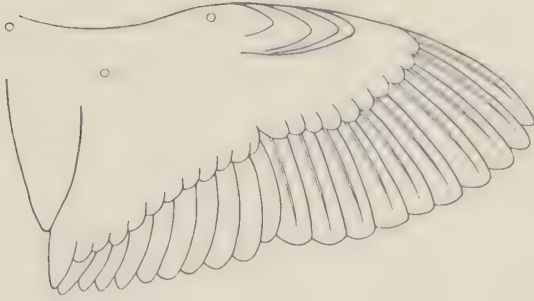


FIG. 15. Outline of the feathered wing of *Turnix tanki*.

comprise about 20% of the body weight. The weight of the “up-beat” muscles (those raising the wing) is about 24% of that of the “down-beat” muscles, versus 15–16% in the Rallidae. Because the active up-beat in hovering flight (“Rüttelflüge”) is useful, especially in the propulsion part of hovering, the size of the “up-beat” muscles is a measure of the rapidity of the take-off.

Based on these comparisons it may be concluded that the Turnicidae are close relatives of the Rallidae. In some respects they are more primitive than the Rallidae but in general they are more advanced and more strongly specialized. They represent, so to speak, an experiment to reach a galliform-like specialization based on the rallid morphology. No characteristics in the wing morphology of the turnicids suggest that these birds should be removed from the Gruiformes to a separate order.

OTIDIDAE

Introduction.—The bustards are a small group of large birds distributed throughout the arid zones of the Old World, including Australia. All are ground birds in the strongest sense of the word. They are fast runners but are not able to spring into the air. Their wings are rather large and broad with well-developed propulsion feathers. The flight is steady, with slow wing beats, but is not very maneuverable. The smallest species (*Tetrax tetrax*) has an energetic take-off and flies with rapid, low amplitude wing beats. *Chlamydotis* flies with slow wing beats at a speed of just over 45 km per hour. The large species fly more rapidly, up to approximately 70 km per hour. None are able to glide. Bustards have 10 primaries, and a vestige of the 11th. The secondaries are diastataxic.

Species studied.—*Otis tarda*, *Chlamydotis undulata*, *Tetrax tetrax*.

Description.—Both the upper and lower arm of the wing are considerably elongated, especially in the larger species (Fig. 16A, B). The skeleton of the manus is very uniformly constructed in the different species. On the whole it is long and narrow and resembles that of the rails, although the individual bones are more massive (Fig. 16A, B). Metacarpus II is not markedly curved. The groove for the tendon of M. ext. dig. communis is much deeper

SYSTEMATIC OBSERVATIONS

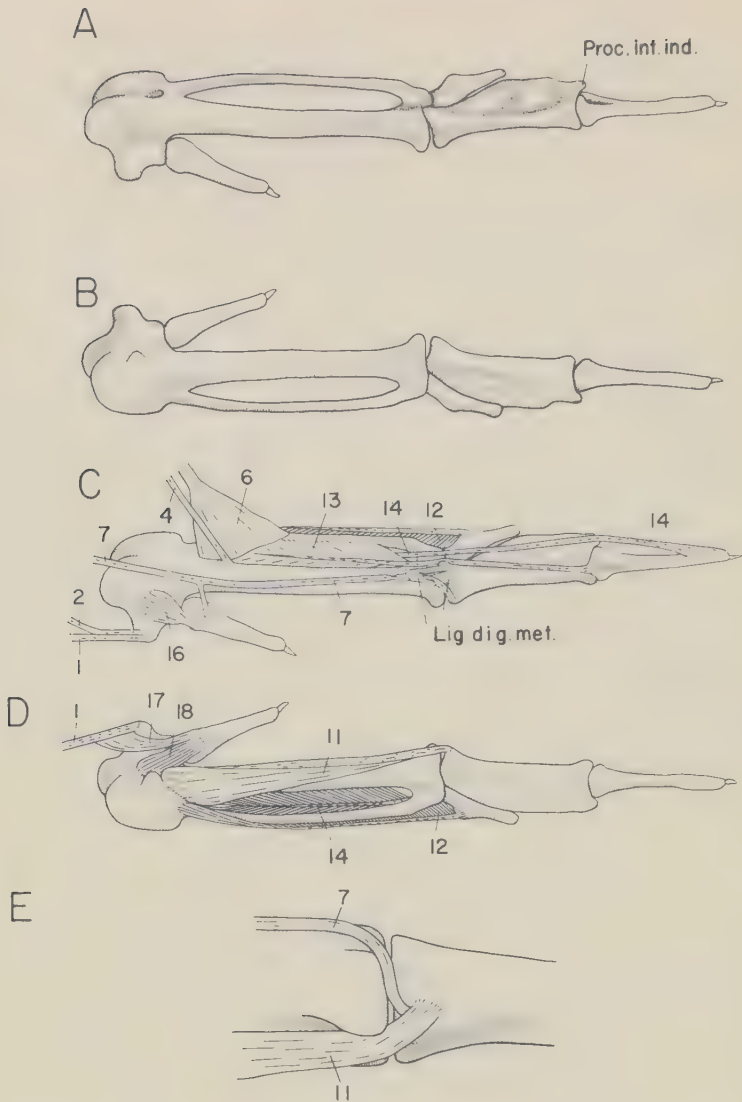


FIG. 16. Manus of *Tetrax tetrax*. (A) Dorsum of the skeleton. (B) Venter of the same. (C) Dorsum of the musculature. (D) Venter of the same. (E) Radial view of metacarpus II.

and more distinct than that in the Rallidae. The distal process is well-developed and its tip is curved ventrally. Metacarpus III is hardly longer than metacarpus II and is very slightly curved so that the intermetacarpal space appears relatively narrow; moreover, it is thin, roundish in cross-section and somewhat broadened and flattened only at the proximal end. The pollex is considerably less than half as long as metacarpus II. It has a well-developed, but rather small, second phalange with a pointed claw; the second phalange is only about

GRUIFORMES

two-thirds the length of that in the rails. The basal phalange of digit II is rather narrow, but strong with well-developed sculpturing on its dorsal surface. It has a well-developed, although not large, internal index process (*Proc. internus indicis*) on its distal end (Fig. 16A). In addition, on its ulnar edge is a distinct protrusion where the cross-ridge of the dorsal surface reaches the edge of the phalange. This gives digit II a characteristic appearance which is repeated in the Gruidae and in the Charadriiformes. The second phalange of digit II is rather long with a deep groove on its dorsal side. There is a small third phalange with a pointed claw. Digit III is not long, it is laterally flattened, and has a well-developed pointed process like that in the Cuculidae but not so large.

The wing muscles are similar to those of the Rallidae, but are stronger developed and have shorter tendons (Fig. 16C, D, E). The *Lig. humero-carpale* is a strong ribbon; the weak *M. flex. dig. sublimis* originates from its inner edge. The tendons of this muscle and of the *M. flex. dig. profundus* insert on the second phalange of digit II. That of the former muscle extends almost to the distal tip of this phalange. The tendon of the *M. flex. dig. profundus* ossifies in the segment lying next to metacarpus II. The tendons of *M. ext. metacarpi radialis* and of the *M. ext. pollicis longus* insert next to one another, as in the Rallidae. The tendon of the *M. ext. dig. communis* curves sharply before its insertion; its curved portion is fastened in place by a loop of the well-developed *Lig. digito-metacarpale* (Fig. 16C). One part of this ligament connects metacarpus II directly with the base of digit II and does not take part in the loop. The *M. abd. indicis* is large and fleshy; its tendon curves dorsally before inserting, slides over a groove of the distal process, and is partly covered by its hooklike tip (Fig. 16E). The tendon of this muscle covers the site of insertion of the tendon of the *M. ext. dig. communis*.

The *M. flex. dig. III* originates from metacarpus III and extends as a narrow muscular band from the proximal end of the metacarpus to digit III (Fig. 16B). The *M. ulni-metacarpalis dorsalis* is not large; its area of origin occupies no more than one-third of the length of metacarpus III. The pinnate *M. inteross. dorsalis* does not quite reach the distal end of the intermetacarpal space; its tendon runs diagonally over the basal phalange of digit II without curving sharply. The pinnate *M. inteross. palmaris* just reaches the distal end of the intermetacarpal space. Its tendon runs over the tip of the internal index process and thereby is held far away from the edge of the second phalange of digit II, on which it inserts near its distal tip. The set of muscles to the pollex is complete. The *M. abd. pollicis* is not large and reaches only to the base of the pollex. The *M. flex. pollicis* is normally developed.

Discussion.—From the above description it can be seen that the Otididae closely resemble the Rallidae in the morphology of their wings, and that they are basically different from the gallinaceous birds and their allies. The bustards have in common with the rails the general structure of the hand skeleton, the strong development of the *Lig. humero-carpale* (and the weak

SYSTEMATIC OBSERVATIONS

development of the *M. flex. dig. sublimis*), the insertion of the tendons of the *M. ext. metacarpi radialis* and the *M. ext. poll. longus*, the curving of the tendon of the *M. ext. dig. communis*, the presence of a loop of the *Lig. digito-metacarpale*, the curving of the tendon of the *M. ext. dig. communis*, the presence of a loop of the *Lig. digito-metacarpale*, the curving of the tendon of the *M. abd. indicis*, the small *M. ulni-metacarpalis dorsalis*, and the strong development of the *M. flex. pollicis*.

However, it is obvious that the *Otididae* have undergone further evolutionary advancement beyond the *Rallidae*. Digit I is thinner than in the rails, its second phalange is very short, metacarpus II has a deeper groove, digit III is very flattened and has a well-developed process. An internal index process is developed; this is absent in the *Rallidae*. All muscles of the wing are more strongly developed, as is the loop of the *Lig. digito-metacarpale*. The tendon of the *M. abd. indicis* covers the site of insertion of the tendon of the *M. ext. dig. communis*.

Most of these characteristics of the *Otididae* are associated with better flying ability when compared to the *Rallidae*. But if one assumes that the poorly developed flight ability of the *Rallidae* is ancestral, then one must conclude that the greater flying skill of the *Otididae* is an advanced feature. One of the features important for better flight is the internal index process (Stegmann, 1963) which is lacking in the *Rallidae* but is present in the *Otididae*, as well as in all the groups to be described below. Poor development of the second phalange has no bearing on the ability to fly but has to be considered as a progressive character in the *Otididae* when compared to the *Rallidae*.

GRUIDAE

Introduction.—The cranes are a small group of extraordinarily large birds. They are, in many respects, a continuation of the bustards. The cranes are distributed over the Old World and in Australia and North America. They mainly inhabit swampy areas; only two species of the 14 in the family are birds of the steppes. The wings of cranes are longer than those of bustards, but are not so broad. The Gray Crane (*Grus grus*) has a wingspread six times larger than the length of its body trunk, while the width of the wing measures 85% of the trunk length. These percentages are similar to those of the snipe (*Gallinago*) while, for example, in the crows (*Corvus*) the wing is much longer and broader. Of course, the great differences in wing dimensions of these birds do not permit direct conclusions about their flying abilities, but one can still assume that cranes can fly great distances rapidly and have the ability only for rapid flight. This is indeed true. Cranes fly quite fast, but with slow wing beats, and they can cover great distances. They rarely glide and do not seem to use true soaring flight. The rounded wing tip with its well-developed propulsion feathers is possibly an adaptation for take-offs by these large, heavy birds. Cranes have 10 primaries, and a vestige of the 11th (lacking in *Balearica*). The secondaries are diastataxic.

Species studied.—*Grus grus*, *G. japonensis*, *Anthropoides virgo*.

GRUIFORMES

Description.—The arm part of the crane wing is even longer than in the bustards. The skeleton of the manus is very much like that of the bustards, and much longer and narrower than those in all Galliformes and Cuculiformes (Fig. 17A, B). Metacarpus III is slightly broader than that in the bustards and is more flattened at its base. Digit I is much shorter than in the bustards and lacks a second phalange. Digit II is bustard-like, but longer and narrower; the internal index process is better developed than that of the bustards. The second phalange is shorter than the basal one; there is no third phalange. Digit III is noticeably curved toward the radial side and is not so broad as in the bustards with a short, blunt, protruding process.

The cranes also show great similarity to the bustards in the structure of the flight muscles. (Fig. 17C, D, E). The Lig. humero-carpale is well-developed; the small M. flex. dig. sublimis originates from the inner side of the distal half of this ligament. The tendon of the M. flex. dig. sublimis inserts on the second phalange of digit II and continues to the distal end of this phalange. The tendon of the M. ext. dig. communis curves sharply before its insertion; this curve is fixed by a strong loop of the Lig. digito-metacarpale (Fig. 17C). A small bundle of fibers does not take part in this loop. The M. abd. indicis is large. Its tendon curves dorsally before inserting (Fig. 17E) and covers the area of insertion of the tendon of the M. ext. dig. communis. The M. inteross. palmaris is rather long and crosses over to the dorsal side of the carpometacarpus. The M. abd. pollicis is very small and does not reach the tendon of the M. ext. metacarpi radialis. The M. flex. pollicis is normally developed.

Many of the tendons of the wing muscles ossify. The following parts of tendons are ossified in adult *Grus grus* and *G. japonensis*: (a) the segments of the M. flex. dig. profundus and the M. flex. dig. sublimis lying next to metacarpus II; (b) the proximal part of the M. inteross. dorsalis; (c) the segment of the M. ext. indicis longus next to metacarpus II; (d) the distal part of the M. abd. indicis; (e) the lower arm parts of the M. ext. metacarpi radialis, M. ext. pollicis longus, M. ext. dig. communis, M. ext. indicis longus, M. flex. carpi ulnaris, and M. flex. dig. profundus; and even the short tendon of the M. ulni-metacarpalis ventralis. In the young of *Grus grus* and *Anthropoides virgo* the tendon of the last muscle does not ossify and the tendons of the other muscles ossify only partially. This extensive ossification of the tendons differentiates cranes from all other birds, even from those with larger wings. At present it is not possible to suggest a functional significance for this peculiarity.

Discussion.—The cranes are very similar to the bustards in their wing morphology, but the cranes are further advanced in their evolution. They have lost the claw phalanges of digits I and II and have evolved a series of adaptations for long distance flight. In addition, the tendons of several muscles ossify. However, the phylogenetic proximity of the cranes to the bustards and to the rails is clearly evident. One can arrange these families into a natural sequence—Rallidae—Otididae—Gruidae. The Rallidae are still

SYSTEMATIC OBSERVATIONS

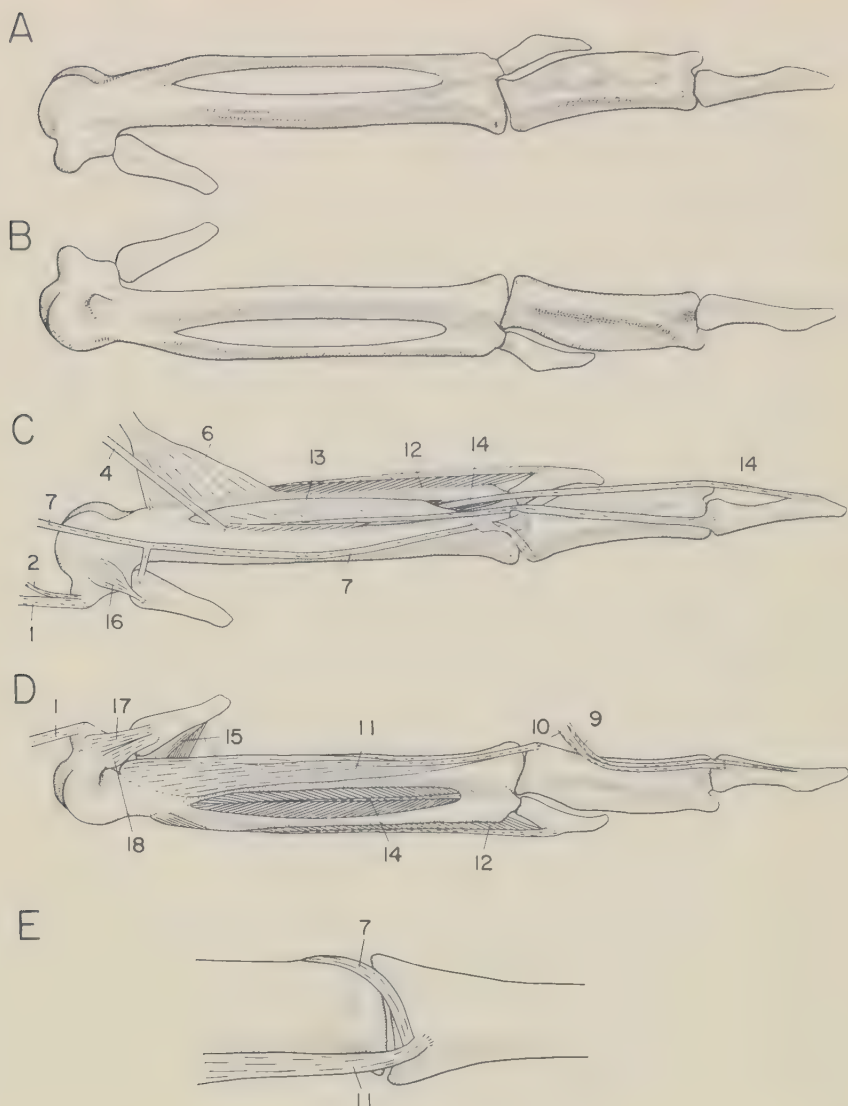


FIG. 17. Manus of *Grus japonensis*. (A) Dorsum of the skeleton. (B) Venter of the same. (C) Dorsum of the musculature. (D) Venter of the same. (E) Radial view of metacarpus II.

very primitive while the cranes form a terminal side branch of the overall group. It seems to be correct to combine these families, together with the Turnicidae and a few other groups, into the order Gruiformes, which is close to the taxonomic groups to be described below but very different from the ones described above (the Galliformes and their allies).

Unfortunately, I was not able to study representatives of the Mesitornithidae (= Mesoenatidae), the Aramididae, the Heliornithidae, or the Rhynochetidae.

GRUIFORMES

EURYPYGIDAE

Introduction.—The sunbittern is a single species of heron-like bird that occurs in tropical forests of South and Central America. It lives on the ground but roosts and breeds in trees. Its wings are relatively large, long, broad, and rounded without propulsion feathers. Flight is supposed to be weak and quiet; undoubtedly the sunbittern flies slowly, agilely, and can ascend vertically, which is necessary for reaching tree limbs in dense swampy forests. They have 10 primaries, and a vestige of the 11th; the secondaries are diastataxic.

Species studied.—*Eurypyga helias*.

Description.—The long bones of the arm are conspicuous in the wing skeleton. The bones of the manus are rather more massive than in the Rallidae and the Gruidae, but much narrower than in the Galliformes (Fig. 18A, B). Metacarpus II is not curved, the groove for the tendon of the M. ext. dig. communis is well-developed, and there is no sign of a muscular tubercle. Metacarpus III is no longer than metacarpus II; it is somewhat broadened and flattened, more curved than in the true Gruiformes, and also somewhat twisted. The pollex is less than half as long as metacarpus II; only a tiny vestige of the claw (phalange II) remains in the skin. The basal phalange of digit II is rather broad, well-sculptured and has a well-developed internal index process, quite similar to that in the Gruiformes. The second phalange is shorter than the first; the third is absent. Digit III is short, laterally compressed, and with a well-developed process, approximately like that in *Turnix* or in the bustards.

The muscles of the wing are not very long (Fig. 18C, D, E). The Lig. humero-carpale is well-developed, and the M. flex. dig. sublimis is, therefore, small and weak. The tendon of this muscle inserts on the second phalange of digit II. The same is true for the tendon of the M. flex. dig. profundus; the latter tendon is completely unossified. The tendon of the M. ext. poll. longus inserts next to the M. flex. dig. profundus; the latter muscle is large and long with a short tendon. The tendon of the M. flex. carpi ulnaris is about one-quarter the length of the muscle, making it relatively long. The tendon of the M. ext. dig. communis curves sharply before insertion and is fixed in place by a well-developed loop of the Lig. digito-metacarpale (Fig. 18C). The M. abd. indicis is long and fleshy; its tendon curves dorsally before its insertion, but it does not cover the site of insertion of the tendon of the M. ext. dig. communis (Fig. 18E). The M. flex. dig. III lies along the entire length of metacarpus III and covers the ventral surface of the proximal end of the intermetacarpal space. The M. ulni-metacarpalis dorsalis is rather large. It extends somewhat beyond the midpoint of metacarpus III and covers the dorsal surface of the proximal end of the intermetacarpal space. The M. inteross. dorsalis reaches the distal end of the intermetacarpal space. Its tendon runs diagonally over the dorsal surface of the basal phalange of digit II without curving and inserts on the second phalange. The M. inteross. palmaris is rather long and reaches the upper side of the carpometacarpus

SYSTEMATIC OBSERVATIONS

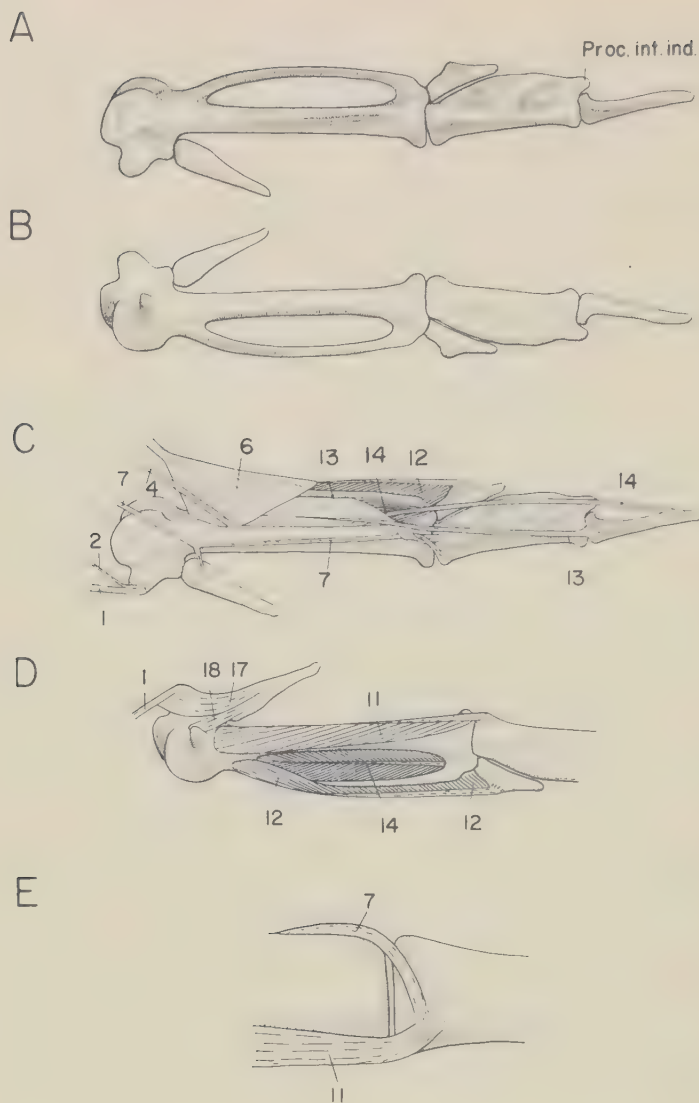


FIG. 18. Manus of *Eurypyga helias*. (A) Dorsum of the skeleton. (B) Venter of the same. (C) Dorsum of the musculature. (D) Venter of the same. (E) Radial view of metacarpus II.

at the level of the articulation of digit III. All muscles to the pollex are present. The *M. abd. pollicis* is large, but its tendon reaches only to the middle of the digit. The *M. flex. pollicis* is normally developed (Fig. 18D).

Discussion.—In general, the wing morphology of *Eurypyga* is similar to that of other members of the Gruiformes and is more advanced than that of the Rallidae. The structure of the basal phalange of digit II puts *Eurypyga*

GRUIFORMES

next to the Otididae and the Gruidae, and the absence of the claw phalanges places both *Eurypyga* and the Gruidae higher than the Otididae. The flattened metacarpus III is generally not characteristic of the Gruiformes, yet is structurally similar to that in *Turnix*. The presence of a Lig. humero-carpale, the insertions of tendons of the M. ext. metacarpi radialis and of the M. ext. poll. longus, the curve of the tendon of the M. ext. dig. communis with a restraining loop of the Lig. digito-metacarpale, and the presence of the M. flex. pollicis all contrast *Eurypyga* and the Gruiformes to the Galliformes and their relatives. The sunbittern forms an independent, well-characterized group with many peculiarities unique to it. It is, therefore, of special interest to demonstrate that in the morphology of the wing the Eurypygidae very clearly belong to the Gruiformes.

CARIAMAE

CARIAMIDAE

Introduction.—The seriemas are a family of only two species, each placed in a separate genus, that are very similar in structure and in their way of life. They live in the brush and high grass of savannas in South America, are very secretive, and fly little and then only over short distances (Frieling, 1936). However, they roost and nest in trees. They are able to rise from the ground in a rapid, steep flight path, and their wings exhibit morphological features that are adaptations for this mode of take-off. In the Cariamidae the flight muscles (M. pectoralis and M. supracoracoideus) are strongly developed, the skeleton of the wing is short and massive, the wings are themselves short, broad, and rounded, the flight feathers stiff, and the propulsive primaries strongly developed. They have 10 primaries without even a rudiment of the 11th. The secondaries have a eutaxic arrangement.

Species studied.—*Cariama cristata*.

Description.—The bones of the manus of *Cariama* (Fig. 19A, B) do not resemble in any way those of the Gruiformes described above, and are much more similar to those of the Galliformes, especially the Cracidae. The carpometacarpus is short and compact, metacarpus II curves ventrally and radially with a small distal process. A rudiment of the muscular tubercle is present. Metacarpus III is very broad and flattened and grooved along the side facing the intermetacarpal space. Moreover, it is strongly curved so that the greatest width of the carpometacarpus occurs at approximately the midpoint of metacarpus III. This metacarpus is twisted so that the outer face of the narrower distal portion is turned toward the ulna and that of the broader proximal part ventrally. The length of digit I is less than half that of metacarpus II. Its second phalange is vestigial, being present apparently only as a horny formation (the horny claw) in the skin. The basal phalange of digit II is broad with well-developed dorsal surface sculpturing, but completely lacks the internal index process. Its ulnar edge is rounded at

SYSTEMATIC OBSERVATIONS

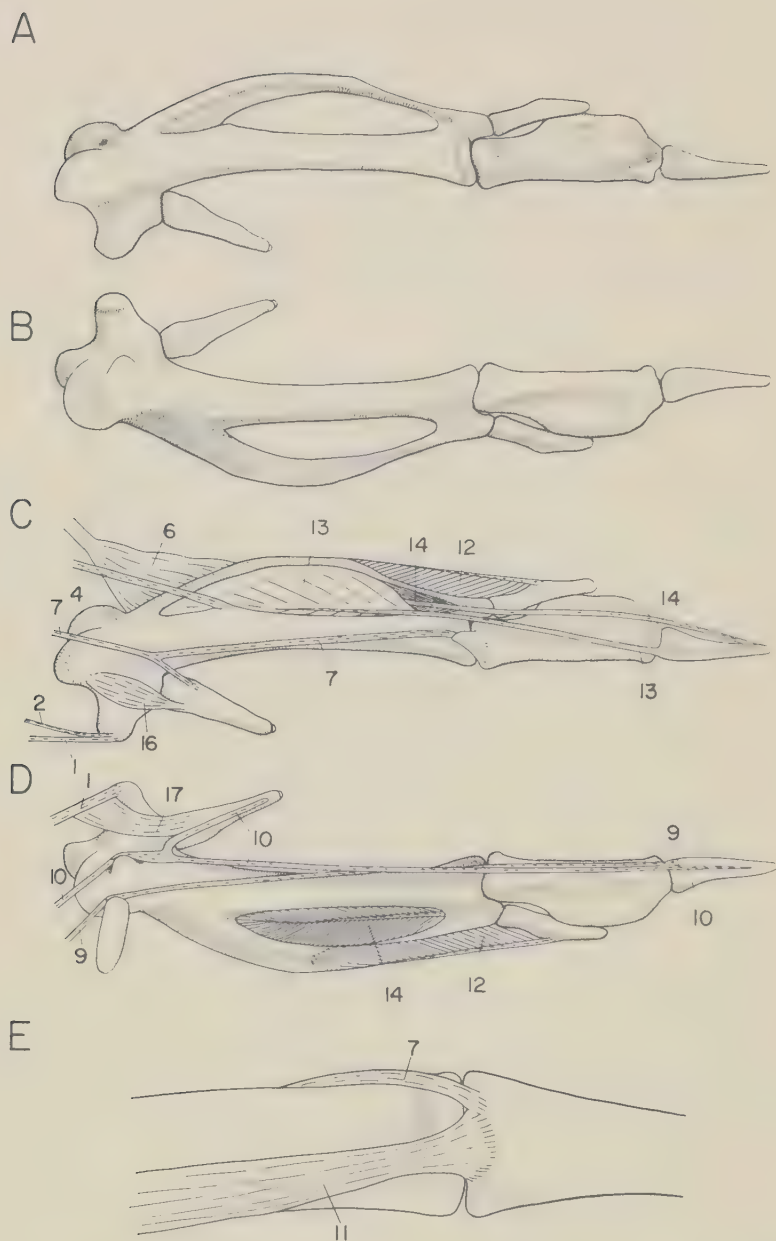


FIG. 19. Manus of *Cariama cristata*. (A) Dorsum of the skeleton. (B) Venter of the same. (C) Dorsum of the musculature. (D) Venter of the same. (E) Radial view of metacarpus II.

GRUIFORMES

the distal end, as in the Galliformes. The second phalange is shorter than the first, and the third is vestigial, as is the pollex. Digit III is long, flattened laterally, and has a small protruding process.

The wing muscles are long and fleshy with short tendons (Fig. 19C, D, E). The tendon of the M. ext. metacarpi radialis is flat and ribbon-shaped. The M. ext. pollicis longus is very large with a short tendon that inserts next to the tendon of the M. ext. metacarpi radialis. The M. flex. carpi ulnaris is thick and fleshy with a very short tendon. The M. flex. dig. sublimis is strongly developed; the Lig. humero-carpale is separated only from the distal part of this muscle and, indeed, from the muscle sheath. In this respect *Cariama* stands, so to speak, between the Gruiformes with a well developed Lig. humero-carpale and the true Alektoromorphae in which the ligament is not developed. The tendon of the M. flex. dig. sublimis inserts on the second phalange of digit II and the tendon of the M. flex. dig. profundus does likewise. The latter sends a broad branch to the pollex; this tendinous branch is stronger than in the Rallidae and extends to the distal tip of the first phalange (Fig. 19D).

The tendon of the M. ext. dig. communis curves slightly ventrally before its insertion; it is attached closer to the dorsal side of digit I than to its ventral side (Fig. 19C, E). The tendon slides over the distal process without being restrained by a loop of the Lig. dig. metacarpale, which does not exist at all. Above the groove of the distal process the tendon is surrounded by a broad layer of connective tissue, which is attached to the pollex as in the Megapodiidae. The M. abductor indicis is large and fleshy, its short tendon inserts without curving; hence, the muscle only abducts digit II without any pronation. Again, this is characteristic of the Galliformes and their allies. The M. flex. dig. III is broad, but short and arises close to the middle of metacarpus III. The M. ulni-metacarpalis dorsalis is rather short, but fleshy, and covers the ventral side of the intermetacarpal space and the original of the M. flex. dig. III. In this area it is difficult to separate the two muscles, as has been mentioned for other very primitive birds. The M. inteross. dorsalis is pinnate; its tendon runs without curving diagonally over the basal phalange of digit II as in the Rallidae and the Cuculidae. The pinnate M. inteross. palmaris is so long that it reaches the dorsal side of the carpometacarpus, but it does not reach the articulation of digit III. The M. abd. pollicis is not large and the M. flex. pollicis is lacking, as in the Galliformes. The tendons of the M. flex. dig. profundus, the M. flex. dig. sublimis, and the M. ext. dig. communis are partly ossified.

Discussion.—The morphology of the wing of *Cariama* is fundamentally different from that of the Gruiformes. Most of the skeletal and muscular characteristics indicate a closer relationship with the Galliformes—*Opisthocomus*—Cuculiformes lineage; in a few features *Cariama* stands between this line and the Gruiformes. The strong development of the branch of the tendon of the M. flex. dig. profundus leading to the pollex ranks *Cariama* far below the Galliformes. The sternum is not galliform-like in *Cariama*, but it is probably

SYSTEMATIC OBSERVATIONS

not so highly specialized as in the latter. Lack of the 11th vestigial primary and the eutaxic arrangement of the secondaries brings *Cariama* close to the Galliformes and their relatives. Clearly, *Cariama* has remained very primitive and shares most of its characters with the true Alektoromorphae. Hence, it is recommended that the Cariamidae be placed at the base of the Alektoromorphae rather than in the Gruiformes where they are generally included.

PSOPHIAE

PSOPHIIDAE

Introduction.—The trumpeters are a small family of three species in a single genus, native to the tropical forests of South America. Usually the Psophiidae are allied with the cranes, mainly because of their long legs. For a long time they have been considered to be close relatives of the Cariamidae, an opinion that was expressed by Stresemann (1927–34). But Wetmore (1960) places these families rather far apart in his Gruiformes. In their external morphology and way of life the Psophiidae are very peculiar. They are ground-dwelling birds, but nest in trees. And they are poor fliers and are not able to fly long distances. The wing is short; the arm portion is especially shortened in comparison to the cranes. The flight feathers are hard and the wing tip strongly rounded. The pectoral muscles are well-developed, with a large *M. supracoracoideus*. All of these features suggest that the trumpeters are able to execute a rapid vertical take-off. The flight of these birds is thus highly specialized and should by no means be labelled as “poor”. The wing is eutaxic with 10 primaries, and no vestigial 11th.

Species studied.—*Psophia viridis*.

Description.—In no way do the bones of the manus of *Psophia* resemble those of the Gruiformes. They are much shorter and more compact (Fig. 20A, B) and show a great similarity to the hand skeleton of the primitive Galliformes and *Cariama*. Metacarpus II is thick and strong, and curves radially as well as ventrally. The groove for the tendon of the *M. ext. dig. communis* is well-developed; at the distal end of the metacarpus the groove is bounded from the radial edge of the bone by a bony elevation that serves to maintain the curve of the tendon, i.e., prevents the tendon from slipping off the metacarpus. A clearly noticeable rudiment of the muscular tubercle is present and is larger than that in *Cariama*. The distal tip of metacarpus III protrudes somewhat toward metacarpus II. Metacarpus III is strongly curved to produce a wide intermetacarpal space, much like that of *Cariama* and the Galliformes. It is flattened and twisted, but is not so broad as in *Cariama* or in the Cracidae. Digit I is about half as long as metacarpus II. Its second phalange is vestigial and is represented only by a tiny structure in the skin, not connected to the basal phalange. Equally vestigial is the third phalange of digit II. The first phalange of digit II is rather broad and

GRUIFORMES

massive, and the ulnar edge of its distal end is rounded as in the Galliformes. There is no hint of an external index process on this bone. The second phalange is shorter than the first, rather broad and compact. Digit III is laterally flattened with a well-developed process, almost like that in the Cuculidae.

The muscles of the lower arm are thick and long (Fig. 20C, D, E) The M. flex. dig. sublimis is large, and the L. humero-carpale is not present.

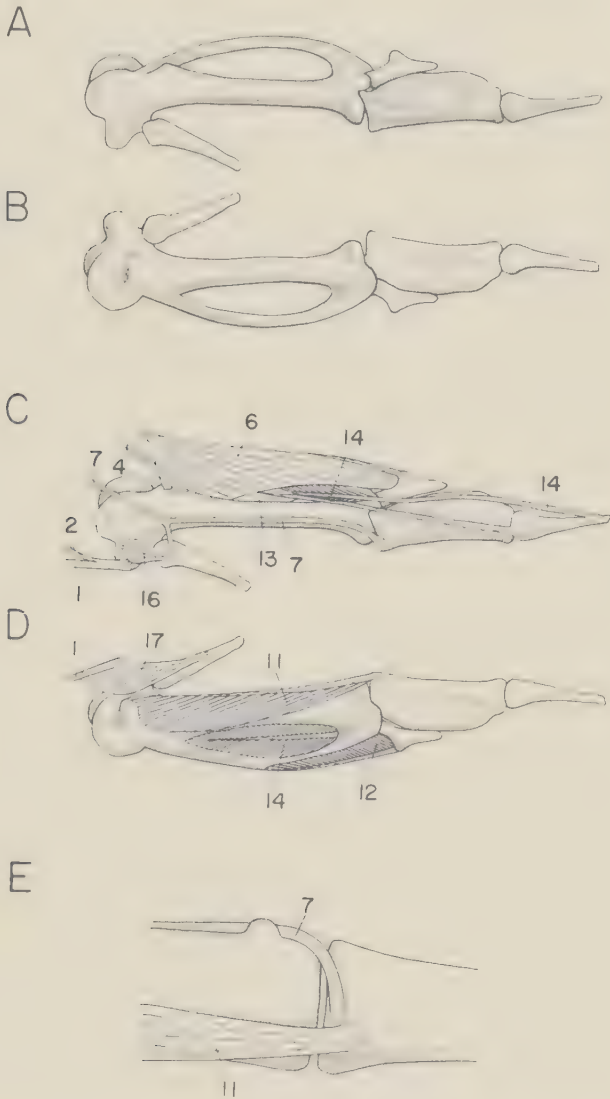


FIG. 20. Manus of *Psophia viridis*. (A) Dorsum of the skeleton. (B) Venter of the same. (C) Dorsum of the musculature. (D) Venter of the same. (E) Radial view of metacarpus II.

SYSTEMATIC OBSERVATIONS

The tendon of this muscle inserts on the second phalange of digit II, as does the tendon of the *M. flex. dig. profundus*. Both tendons ossify in the portion lying next to metacarpus II. The tendon of the *M. ext. metacarpi radialis* is broad and ribbon-shaped, and partially covers the site of insertion of the flat tendon of the *M. ext. poll. longus*. The tendon of the *M. ext. dig. communis* curves sharply before insertion, slides over the distal process, and is retained in place by the bony elevation already described, not by the loop of the *Lig. digito-metacarpale* which is lacking in this genus (Fig. 20C, E). The *M. abd. indicis* is very large and its tendon inserts on the dorsal surface of digit II without curving; hence, contraction of this muscle abducts the second finger without pronating it. The tendon of the *M. ext. dig. communis* inserts directly next to that of the *M. abd. indicis*, but is not covered by it. The *M. flex. dig. III* is fleshy, but short and originates from the middle of metacarpus III. The *M. ulni-metacarpalis dorsalis* is of maximum size. On the dorsal side of the carpometacarpus it reaches digit III; its fleshy insertion covers the largest part of the intermetacarpal space. On the ventral side of the hand this muscle reaches to the middle of metacarpus III and also partly covers the intermetacarpal space.

The pinnate *M. inteross. dorsalis* is noticeably shorter than the intermetacarpal space; its tendon runs diagonally over the dorsal surface of the basal phalange of digit II without curving radially. The *M. inteross. palmaris* is long and reaches the articulation of digit III on the dorsal side of the carpometacarpus. The *M. abd. pollicis* is large, but its tendon does not reach as far as the tip of the pollex. The *M. flex. pollicis* is absent (Fig. 20D).

Discussion.—A comparison of the hand morphology of *Psophia* and *Cariama* supports the conclusion of the classical morphologists. Even though the *Psophiidae* may be a distinct group, they are closest to the *Cariamidae*. And, just like the latter group, the *Psophiidae* do not belong to the *Gruiformes*, but are much closer to the *Galliformes*. They have a short carpometacarpus, as do the gallinaceous birds, without an internal index process, a strong *M. flex. dig. sublimis* but no *Lig. humero-carpale*, and flat tendons of the *M. flex. metacarpi radialis* and the *M. ext. poll. longus*. The curve of the tendon of the *M. ext. dig. communis* is maintained by the distal process without the assistance of the loop of the *Lig. digito-metacarpale*, which is completely lacking. The *M. ulni-metacarpalis dorsalis* is strongly developed but the *M. flex. pollicis* is absent.

This whole complex of characteristics is typical of the *Tinamiformes*–*Galliformes*–*Cuculiformes* lineage and very different from the morphology of the *Gruiformes*–*Charadriiformes* complex. The relationship between the *Psophiidae* and the *Cariamidae* is, of course, not very close. In general, the *Cariamidae* are clearly more primitive. They have such ancient features as, for instance, a branch of the tendon of the *M. flex. dig. profundus* that inserts on the pollex. The curve of the tendon of the *M. ext. dig. communis* is very slight in *Cariama*, while it is well-developed in *Psophia*. The *M. ulni-metacarpalis dorsalis* in *Psophia* is extremely well-developed, while it has remained primitive

CHARADRIIFORMES

in *Cariama*. If one assumes that *Cariama* is placed at the base of the Alektoromorphae, hardly more advanced than the Tinamidae, then *Psophia* has evolved almost as much as the primitive Galliformes without, of course, belonging to this group. The lack of the 11th primary and the eutaxic arrangement of the secondaries are also characteristics of the true Alektoromorphae.

CHARADRIIFORMES

The shorebirds, gulls, terns, and their allies are a large group of birds that show a clear-cut relationship to the Gruiformes (Lowe, 1931), but are, in general, evolutionarily more advanced than the latter group. The members of the Charadriiformes have, with the exception of a number of aberrant forms, relatively narrow, pointed wings which enable them to fly long distances rapidly. All have 10 primaries, and a vestige of the 11th. The secondaries are diastataxic.

CHARADRII (LIMICOLAE)

The charadriids, or true shorebirds, are found throughout the world. This is the most species-rich group in the order. Most species are restricted to swampy areas or to the vicinity of water of some type, but others live in dry plains and deserts. All fly rapidly and some fly enormous distances without stopping. Their wings are moderately long, but very narrow and pointed which makes them appear even longer. The arm portion of the wing is noticeably elongated. This feature may be a historical inheritance, but rather than being a disadvantage, it is an advantage for rapid flight (Stegmann, 1962).

The skeleton of the manus is uniformly constructed in all members of this group. It is long and narrow and, in general, shows similarities with that of the Gruiformes. Metacarpus II has a deep groove. The distal process lies closer to the ventral surface of metacarpus II than to its dorsal surface; it has a groove and a ventrally curved tip for the retention of the tendon of the M. abd. indicis. Metacarpus III is very narrow and thin distally and becomes broader only at its proximal end. The basal phalange of digit II is rather broad, with a well-developed internal index process, prior to which the phalange is constricted slightly. This shape of the first phalange of digit II is characteristic of the Otididae and the Gruidae, but is even more strongly developed in the Charadrii. The second phalange is long, yet still shorter than the basal phalange. Usually a vestige of the third phalange remains. The pollex always has a second phalange with a pointed claw, but in some species it is vestigial. Digit III is short, noticeably curved radially, and has almost no projections. The peculiar form of digit III is characteristic of all Charadrii and is not much modified throughout the order.

CHARADRIIDAE

The details of the wing morphology in this large, diverse family will be discussed under the headings of the several subfamilies.

SYSTEMATIC OBSERVATIONS

Charadriinae

Introduction.—The plovers, because of their structure and feeding habits, are considered to be one of the least specialized subgroups of the Charadriidae and to have retained the greatest number of ancient features among the Limicolae. With respect to flight, the plovers are reasonably highly specialized. They fly with great speed and can cover very long distances without stopping. These aspects of flight are developed in the plovers at the expense of other features. Their flight is not agile, nor are these birds able to start with a rapid, steep take-off. Consequently, the up-beat muscles are relatively weakly developed (15-16% of the weight of the down-beat muscles compared to 24% in the woodcock, *Scolopax*). The wings of plovers are narrower and more pointed than those in all other Limicolae.

Species studied.—*Pluvialis (Squatarola) squatarola*, *Pluvialis apricaria*, *Charadrius hiaticula*, *Eudromias morinellus*.

Description.—The skeleton of the manus is like that in all Limicolae, but the second phalange of digit I is larger than in other members of this family (Fig. 21A). The structure of the wing muscles is very uniform in all species investigated (Fig. 21B, C, D). In general, the wing muscles are moderately large, which is especially conspicuous since the bones are rather long. The M. ext. metacarpi radialis has a long tendon which is as long as the fleshy part. The M. ext. poll. longus is small. It covers the proximal part of the radius and has a thin tendon that joins the tendon of the M. ext. metacarpi radialis before their common insertion. The M. flex. carpi ulnaris is rather thin and weak, and its tendon is not less than one-fourth the length of the ulna. The Lig. humero-carpale is well-developed and forms a broad band. The M. flex. dig. sublimis is small and originates from the inner side of the band; the tendon of this muscle inserts on the second phalange of digit II and continues as a thin thread as far as the vestige of the third phalange. A similar arrangement of this tendon occurs in *Squatarola* and *Pluvialis*. In *Charadrius* the portion of the tendon attached to the second phalange is isolated from the main tendon so that it represents a functionless vestige. The M. flex. dig. profundus is not large, it is restricted to the proximal end of the lower arm, and it has a long tendon that does not ossify.

The M. flex. metacarpi ulnaris is large and extends over almost the whole lower arm. The M. ext. dig. communis is short and is limited to the proximal part of the lower arm; it has a very long tendon. Before its insertion the tendon curves, but only moderately (Fig. 21B, D). The Lig. digito-metacarpale is well-developed, but only a small part of it goes over the tendon in the form of a loop; the greater part of the ligament simply connects the digit with metacarpus II. The cross-over site of the tendon and the ligament is surrounded by connective tissue that is attached to the basal phalange of digit II. The M. abd. indicis is large and fleshy with a very short tendon that curves dorsally before its insertion; the curved tendon glides over the groove of the distal process (Fig. 21D). The M. flex. dig. III originates on

CHARADRIIFORMES

the outermost edge of the proximal end of metacarpus III; it is a small ribbon that reaches digit III. The M. ulni-metacarpalis dorsalis is not large and inserts over the proximal third of metacarpus III. It covers the proximal part of the M. flex. dig. III.

The pinnate M. inteross. dorsalis reaches the end of the intermetacarpal space; its tendon extends diagonally in a straight line over the first phalange of digit II. The pinnate M. inteross. palmaris also reaches the end of the intermetacarpal space. All four muscles of the pollex are normally developed. The M. flex. pollicis is quite large (Fig. 21C). The tendon of the M. abductor pollicis almost reaches the tip of digit I.

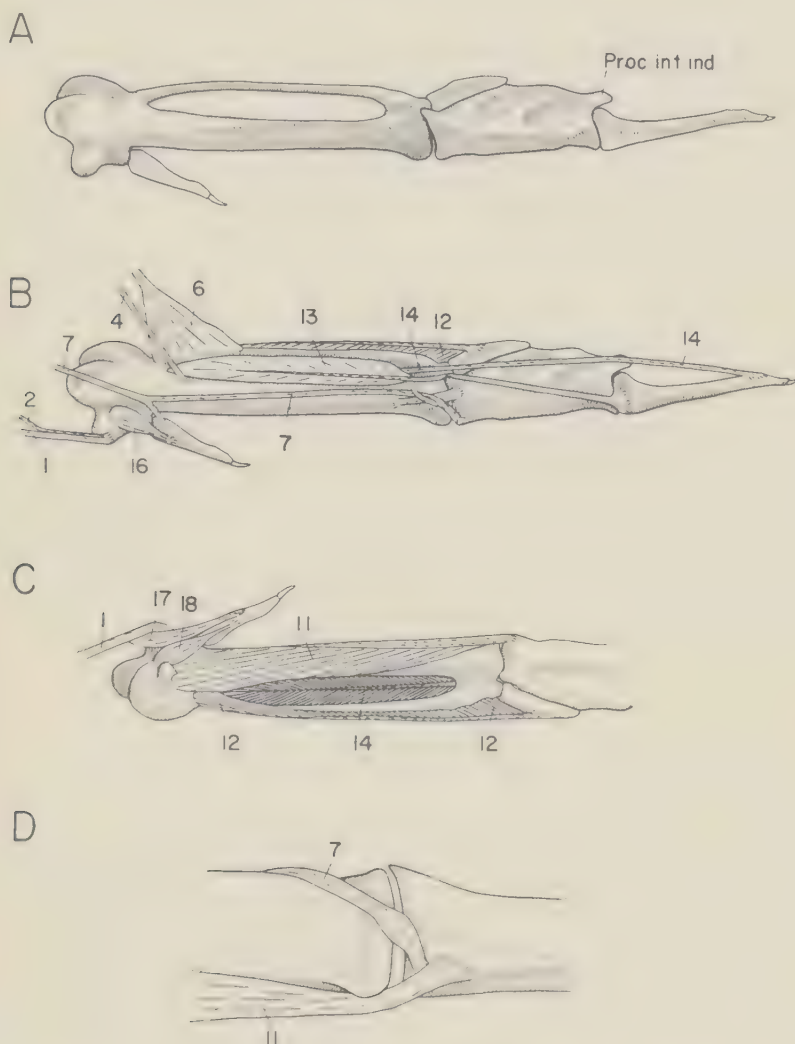


FIG. 21. Manus of *Pluvialis apricaria*. (A) Dorsum of the skeleton. (B) Dorsum of the musculature. (C) Venter of the same. (D) Radial view of metacarpus II.

SYSTEMATIC OBSERVATIONS

Vanellinae

Introduction.—The lapwings are a small group of birds that are undoubtedly closely related to the plovers. Their wings are longer and broader with a broad, rounded tip. The arm of the wing is elongated. Some species have a pointed spur at its bend. The European Lapwing (*V. vanellus*) does not have the spur, but has a dull process on the Proc. metacarpi I which is covered with hard horny skin that undoubtedly serves as a weapon.

Species studied.—*Vanellus vanellus*, *V. (Chettusia) gregarius*.

Description.—The bones of the wing of the lapwings differ from those of the plovers only by their greater length. The claw on digit I is very small, that on digit II is hardly visible. The M. flex. pollicis longus is longer and its tendon is shorter. The tendon of the M. ext. dig. communis curves more before its insertion, and the loop of the Lig. digito-metacarpale is formed by a greater mass of fibers.

Discussion.—All of these features show that the lapwings are more advanced in the evolution of their wing than the plovers, from which they descended as an aberrant group.

Calidridinae

Species studied.—*Calidris alpina*, *C. ferruginea*, *C. temminckii*, *C. maritima*, *Philomachus pugnax*, *Limicola falcinellus*.

Discussion.—The members of this group are very similar to the plovers, and especially to the vanellines, in the features mentioned above. In addition, they have a well-developed claw on digit I. The curve of the tendon of the M. ext. dig. communis is slight with only a small number of fibers participating in the formation of the loop of the Lig. digito-metacarpale. Vestiges of the tendons of the M. flex. dig. sublimis and of the M. inteross. dorsalis are found on the second phalange of digit II.

Tringinae

Species studied.—*Tringa nebularia*, *T. ochropus*, *T. glareola*, *Actitis hypoleucos*, *Xenus cinereus*.

Discussion.—This group is somewhat further removed from the plovers. They have a much smaller claw on the pollex, which is often vestigial; the claw on digit II may be lacking completely. The curve of the tendon of the M. ext. dig. communis is sharper than in the previous group, and the loop of the Lig. digito-metacarpus is more strongly developed as most of the fibers of this ligament take part in its formation (Fig. 22A). A vestige of the tendon of the M. flex. dig. sublimis is still found on the second phalange of digit II, but that of the tendon of the M. inteross. dorsalis is either extremely small or completely lacking. The tendon of the M. abd. pollicis does not insert at the tip of digit I, but usually at the middle.

CHARADRIIFORMES

Scolopacinae

Species studied.—*Gallinago gallinago*, *G. stenura*, *Lymnocyrtus minimus*, *Scolopax rusticola*.

Discussion.—The woodcocks and snipe are even further removed from the plovers than are the tringines. The claw on digit I is vestigial and is often lacking on digit II. The tendon of the M. abd. pollicis is short and usually does not reach the middle of the pollex. The vestige of the tendon

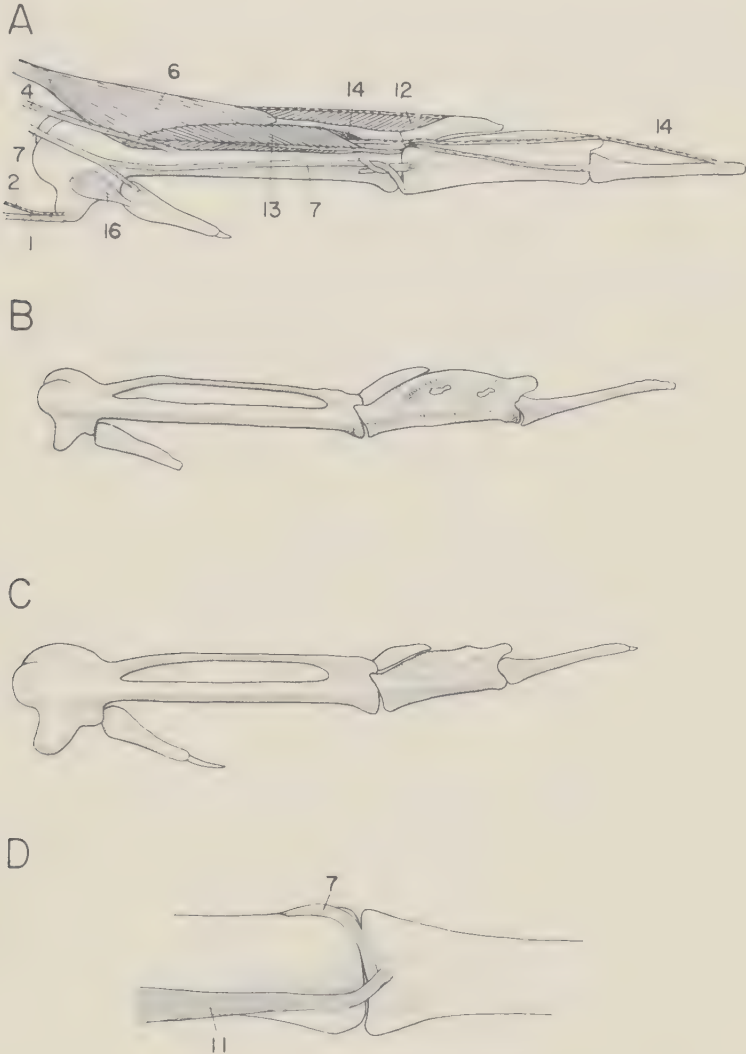


FIG. 22. (A) Dorsum of the musculature of the manus of *Tringa nebularia*. (B) Dorsum of the skeleton of the manus of *Cursorius cursor*. (C) Dorsum of the skeleton of the manus of *Glareola nordmanni*. (D) Radial view of metacarpus II of *Scolopax rusticola*.

SYSTEMATIC OBSERVATIONS

of the *M. flex. sublimis* that is attached to the second phalange of digit II is in varied stages of ossification in different species, and even in different specimens of the same species; the tendon is modified into a protruding ledge of bone. The vestige of the tendon of the *M. inteross. dorsalis* is lacking. In general, the muscles of the wing of the scolopacines are more strongly developed than in the former groups and the tendons are, consequently, shorter. The tendon of the *M. ext. dig. communis* curves even more sharply prior to its insertion (Fig. 22D) and the loop of the Lig. digito-metacarpale is more strongly developed than in the previously described groups, yet the difference from *Tringa* is not great. In the woodcock (*Scolopax*), which has the most highly developed rapid, steep take-off in this subfamily, the tendon of the *M. flex. dig. profundus* is always ossified in the segment lying next to metacarpus II.

DISCUSSION

Analysis of the great mass of comparative data for the Limicolae leads to the following conclusions. Members of this large species-rich group have a great uniformity in the morphology of the manus of the wing, in spite of the large differences in their general appearance, in their feeding adaptations (Kozlova, 1961–1962; Judin, 1965), and in the characteristics of their flight (Stegmann, 1962). Even such aberrant forms as *Vanellus*, *Numenius*, *Haematopus*, and *Himantopus* can hardly be distinguished from the typical members of the Limicolae in regard to the morphology of the manus.

GLAREOLIDAE

Introduction.—This small group of waders consists of species of very different appearance and way of life. They are distributed over the steppes and deserts of the Old World, including Australia. The flight characteristics, as well as the external morphology of the wing, are very different in *Cursorius* and in *Glareola*, which are typical of the two main types in this family.

Species studied.—*Cursorius cursor*, *Glareola pratincola*, *G. nordmanni*.

Description.—Both genera are easily recognized as charadriiform birds by the morphology of their wings (Fig. 22B, C). The basal phalange of digit II is similar to that of the plovers, with a well-developed internal index process and a protrusion in the middle of the ulnar surface. Digit III is slightly curved radially; it is pointed and practically without any process. The tendon of the *M. ext. dig. communis* curves sharply before its insertion (Fig. 23A, B). The loop of the Lig. digito-metacarpale is well-developed. The second phalange of digit II lacks vestigial tendons.

However, differences exist between the two genera in the morphology of their wings; in *Cursorius* the second phalange of digit I is well-developed and the claw is larger than in all other Charadrii and almost like that in the Rallidae (Fig. 22C). The second phalange of digit II is similar to that in the Charadriidae. The tendon of the *M. abd. indicis* is long and reaches

CHARADRIIFORMES

the second phalange of digit I. The tendons of the *M. ext. dig. communis* and of the *M. abd. indicis* insert next to one another (Fig. 23A). In *Glareola* the second phalange of digit I is extremely vestigial and appears to be present only in the skin (Fig. 22B). The tendon of the *M. abd. pollicis* is short and does not reach the middle of the pollex. The tendon of the *M. abd. indicis* covers the site of insertion of the tendon of the *M. ext. dig. communis* (Fig. 23B). The internal index process of the first phalange is larger than that in all other Limicolae and is more similar to that in the gulls. The plate of the first phalange is perforated in two places (in the proximal and in the distal part) which again is similar to that in the gulls.

Discussion.—It is clear that in a number of characteristics *Cursorius* is more primitive than *Glareola*. The latter is more specialized and represents a very aberrant group, far removed from the average type of the Limicolae. The peculiarities of *Glareola*, which appear to indicate a similarity to the gulls and terns, are obviously the result of parallel evolution. The strong development of the internal index process is, in both cases, associated with the presence of a very long 10th (distal) primary (Stegmann, 1963). Likewise, the perforated plate of the basal phalange of digit II appears to be correlated in some way with extremely long distal primaries (8th and 9th). This feature is first seen in *Glareola*, then in the Larinae, is even more specialized in the Sterninae, and, finally, also occurs in the Caprimulgidae, the Apodidae, and the Trochilidae. Thus, it would be incorrect to interpret the peculiarities of *Glareola* as an approach to the Laridae.

The great difference in the morphology of the wing between *Glareola* and *Cursorius* completely justifies the division of the Glareolidae into two subfamilies. If one adds the differences in the external morphology and in the way of life, it might be concluded that *Glareola* and *Cursorius* are members of two distinct families. Unfortunately I was not able to study other members of this group that may possibly bridge the morphological gap between *Cursorius* and *Glareola*.

BURHINIDAE

Introduction.—The thick-knees are a small group of birds that are, in general, similar to the Limicolae, but in some respects resemble the bustards. They inhabit the dry zones of the Old World, America, and Australia. They are ground-dwelling birds that are not able to perch in trees. Their flight is easy, but not fast: it is more agile than in bustards and not so fast as that of the Limicolae. The burhinids fly easily up from the ground, but move with rather slow wing beats and often glide. The wings are long, especially in the arm, broad for Limicolae, and not very pointed.

Species studied.—*Burhinus oedicephalus*.

Description.—In the wing skeleton the lower arm is longer than the manus (Fig. 23C, D). The groove on metacarpus II is very well-developed in the charadriids, but is distinct only in the distal end of the bone in *Burhinus*:

SYSTEMATIC OBSERVATIONS

this groove is flattened and indistinct at its proximal end. Metacarpus III is very narrow and is broadened and flattened only at its proximal end. Digit III is laterally flattened and has a well-developed process (Fig. 23C). In all these characteristics the thick-knees resemble the bustards more than the Limicolae. Digit I has a long, somewhat curved, second phalanx which

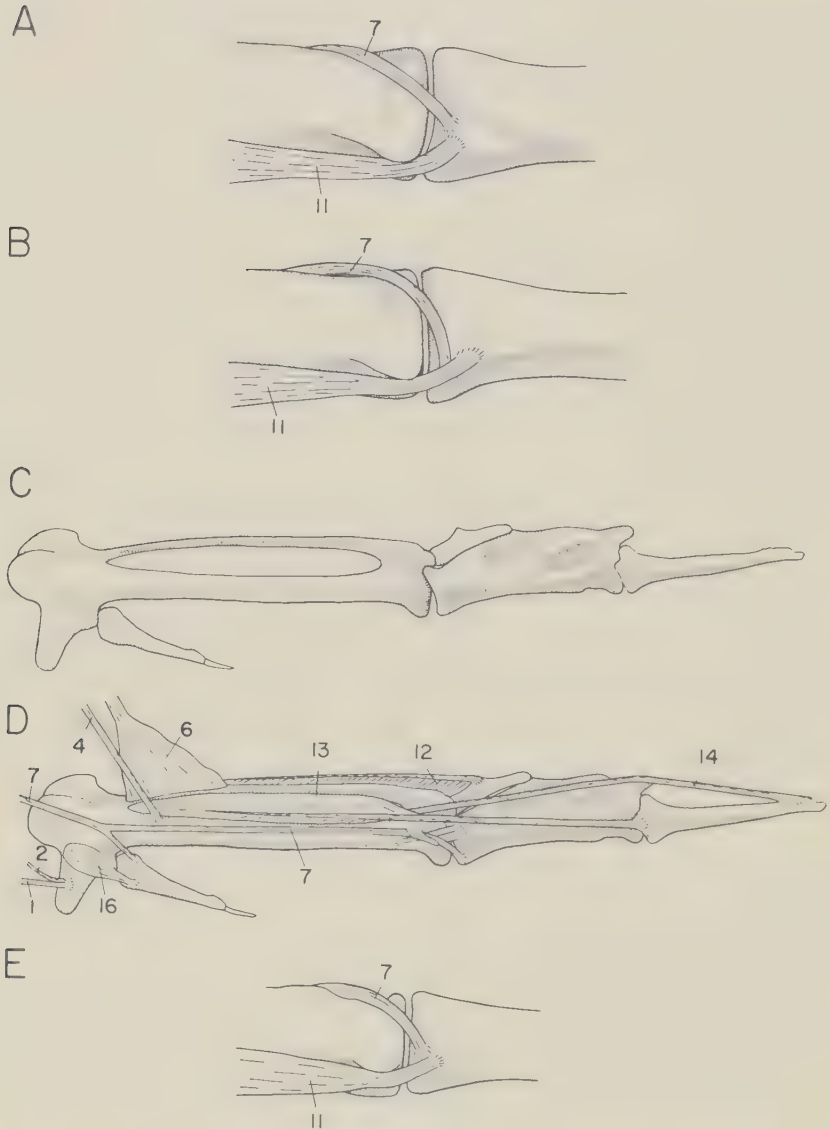


FIG. 23. (A) Radial view of metacarpus II of *Cursorius cursor*. (B) Radial view of metacarpus II of *Glareola nordmanni*. (C) Dorsum of the skeleton of the manus of *Burhinus oedicnemus*. (D) Dorsum of the manus of *Burhinus oedicnemus* showing the musculature. (E) Radial view of metacarpus II of *Burhinus oedicnemus*.

CHARADRIIFORMES

is longer than that in the bustards, as well as in the Limicolae (except *Cursorius*). The process of metacarpus I has a lumpy elevation, which obviously serves as a weapon.

The tendons of the M. inteross. dorsalis and the M. inteross. palmaris are only fastened by connective tissue to the distal end of metacarpus II, as in the bustards. This is different from the Limicolae that have horizontal bony ledges at the distal end of the metacarpus which may unite into a bony bridge. In *Scolopax* there is a second bony bridge at the distal part of the basal phalange of digit II. It serves to fasten the tendon of the M. inteross. dorsalis. In this respect *Burhinus* is clearly more primitive than the Limicolae, and ranks approximately at the evolutionary stage of the bustards.

The burhinids are rather nondistinct in the morphological development of their wing muscles, yet they clearly belong to the lineage of Gruiformes-Charadriiformes. The Lig. humero-carpale is very well-developed and the M. flex. dig. sublimis is small and originates from the inner side of this ligament. The M. ext. metacarpi radialis is short with a very long tendon. The M. ext. poll. longus, on the other hand, is rather long with a short tendon. The M. ext. dig. communis is moderately large, its tendon is fastened at its curve with a well-developed loop of the Lig. digito-metacarpale (Fig. 23). The M. abd. indicis is large and its tendon curves dorsally; however, it does not cross the tendon of the M. ext. dig. communis, as is the case in the Limicolae, but it is attached next to it as in the bustards (Fig. 23E).

The tendons of the M. flex. dig. sublimis and of the M. flex. dig. profundus both insert on the second phalange of digit II. On the second phalange is a noticeable vestige of the tendon of the M. inteross. dorsalis. The M. flex. dig. III extends as a narrow ribbon along the entire metacarpus III. The M. ulni-metacarpalis dorsalis is small. The M. inteross. dorsalis almost reaches the distal end of the intermetacarpal space; its tendon runs diagonally over the basal phalange of digit II. The M. inteross. palmaris is just as long as the former muscle. All four muscles of the pollex are normally developed. The M. abd. pollicis is large and reaches the second phalange of digit I.

Discussion.—It can be seen that in the anatomy of the wing there are differences between *Burhinus* and the Limicolae; in general, the wing of *Burhinus* is more primitive than that of the Limicolae and tends more toward that of the Otididae, although it is somewhat different. It appears that the Burhinidae are intermediate between the Gruiformes and the Charadriiformes, as had been already concluded by Fürbringer (1888). But it is not possible to decide at this time into which order the Burhinidae should be placed.

JACANIDAE

Introduction.—The jacanas are a small group of peculiar birds that are distributed in the tropics of all continents. At first sight the jacanids seem to resemble the Rallidae, mainly because of their long toes and claws. In reality, however, they are far removed from the Rallidae, not only in their

SYSTEMATIC OBSERVATIONS

body structure but also in their way of life. They live on small lakes and lagoons that are covered with floating vegetation, walking skillfully on floating leaves, and flying up frequently to cross areas of open water. They are able to rise and descend vertically. The wings of these birds are large, broad, and rounded, but the propulsion feathers are not well-developed. They have 10 primaries, and a vestige of the 11th; the secondaries are diastataxic.

Species studied.—*Jacana spinosa*, *Actophilornis africana*.

Description.—The arm segment of the wing skeleton is clearly elongated, as is characteristic for the Limicolae (Fig. 24A, B). All species have a large curved spur on the process of metacarpus I which is connected to the muscular process of the metacarpus (Proc. muscularis metacarpi) by a bony ridge, under which runs the tendon of the M. flex. dig. profundus (Fig. 24A, B). At the distal part of the intermetacarpal space the carpometacarpus is perforated for the tendon of the M. inteross. palmaris, which runs first through a deep groove on the distal part of carpometacarpus and then along the basal phalange of digit II. Thus, the first phalange of digit II is broadened and there is an elevation on the ulnar edge of the groove which partly covers it. Digit I is radically broadened, it has a well-developed second phalange with a pointed, somewhat curved claw. A tiny vestige of the claw phalange exists on digit II; it might be lacking in some individuals. Digit III is short, laterally compressed, somewhat radically curved, and has a short protruding process. It is partly covered by the broad first phalange of digit II.

The M. ext. metacarpi radialis is short with a long moderately flattened tendon. On the other hand, the M. ext. poll. longus is long with a short tendon which inserts next to the tendon of the former muscle (Fig. 24C, D, 25A, B). The two tendons join just prior to their insertion. The M. flex. carpi ulnaris is fleshy over its entire length, with a very short tendon. The Lig. humero-carpale is well-developed; accordingly, the M. flex. dig. sublimis is small and weak. On the other hand, the M. flex. dig. profundus is very large and extends over almost the entire length of the lower arm. The tendons of both muscles insert on the second phalange of digit II; that of the M. flex. dig. sublimis is very thin, while that of the M. flex. dig. profundus is thick, strong, and ossifies in the segment next to metacarpus II. In young specimens of *Jacana spinosa* ossification of this tendon is less pronounced than in adult birds.

The M. flex. metacarpi ulnaris is unusually large and fills the entire inner side of the curve of the ulna. The M. ext. dig. communis is also large and covers the entire lower arm. Its tendon curves sharply before insertion and is held in place by a loop of the Lig. digito-metacarpale (Fig. 24C). The M. abd. indicis is very large; its tendon curves dorsally before insertion and glides over the distal process. It covers the area of insertion of the M. ext. dig. communis (Fig. 25A). The M. ulni-metacarpalis dorsalis is rather large. It reaches to the middle of metacarpus III and is thick and fleshy. The M. flex. dig. III is extremely well-developed. It originates from the proximal end of the intermetacarpal space with a thick fleshy muscle that

CHARADRIIFORMES

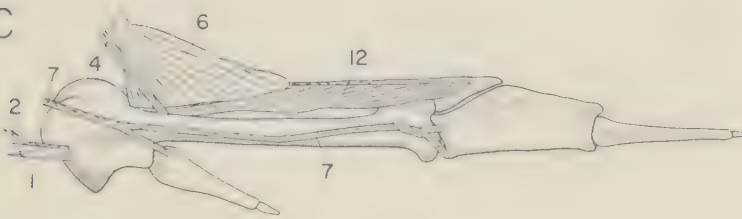
A



B



C



D

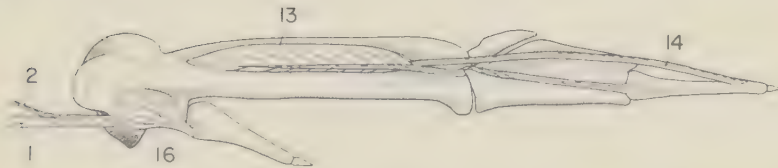


FIG. 24. Manus of *Jacana spinosa*. (A) Dorsum of the skeleton. (B) Venter of the same. (C) Dorsum of the superficial musculature layer. (D) Dorsum of the deeper musculature layer.

reaches as far as digit III (Fig. 24D). The M. inteross. dorsalis also reaches the distal end of the intermetacarpal space. Its tendon runs diagonally over the basal phalange of digit II. The M. inteross. palmaris is equally long; its tendon passes through the channel described above and extends farther through the groove of the carpometacarpus and along the first phalange of digit II. Here it is partially covered by the elevation of this bone so that the tendon cannot slide off laterally. It is probable that this attachment is an adaptation for very frequent vertical take-offs, allowing alternate loads with very different positions of the wing. The pollex has a complete set

SYSTEMATIC OBSERVATIONS

of muscles. The tendon of the *M. abd. pollicis* extends to the second phalange of digit I (Fig. 25B).

Discussion.—From the above description it is clear that the family Jacanidae has nothing in common with the Rallidae, and belongs unquestionably to the Charadriiformes. But the jacanas are an isolated group in the latter order, both in their way of life as well as in their morphology. The necessity for frequent vertical take-off and alighting, often on an unstable surface and in the forest amid trees, lead to the evolution of the characteristic flight apparatus described. In order to fly sufficiently slowly, and not to hurry along as do the Limicolae, the surface of the wing had to be enlarged by broadening. It may be added that in the Jacanidae the main upstroke muscle of the wing (the *M. supracoracoideus*) is very large, as it seems to be essential for well-developed hovering flight.

Because of the large claw on digit I, the Jacanidae appear to be more primitive than the Limicolae, but in other respects they are more advanced, as, for instance, in the development of the loop of the Lig. digito-metacarpale. It seems, therefore, that the jacanas have evolved parallel to the Limicolae for a long time and should be regarded as a taxonomic group of equal rank. It is a matter of personal preference whether to place them before or after the Charadriidae.

CHIONIDIDAE

Introduction.—The sheathbills are a small family of two closely related species placed in a single genus, *Chionis*. These birds live on subantarctic islands along the shore and feed on whatever debris that can be found,

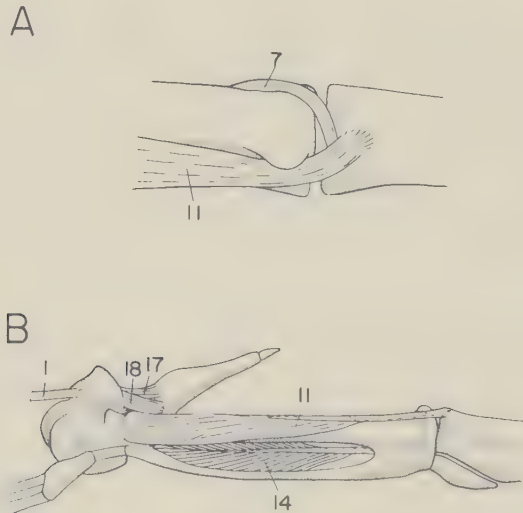


FIG. 25. Manus of *Jacana spinosa*. (A) Radial view of metacarpus II. (B) Venter of the musculature.

CHARADRIIFORMES

as well as by robbing the nests of seabirds. Sheathbills walk well and can also run; they lack webs on the feet and do not give the impression of being seabirds. They fly with relatively rapid wing beats (pigeon-like), take off easily, and fly even within limited spaces. But they are also able to fly long distances and migrate in winter over open water for hundreds and even thousands of kilometers. The wings are short, rather broad, and only slightly pointed, quite unlike those of seabirds. In fact, sheathbills resemble pigeons. They have 10 primaries, and a vestige of the 11th. The secondaries are diastataxic.

Species studied.—*Chionis alba*.

Description.—The bones of the wing are shorter than those in the plovers, but longer than those of the pigeons and Galliformes. The skeleton of the manus is slightly more compact than in the Limicolae (Fig. 26A, B). Metacarpus II has a deep groove and metacarpus III is very plover-like, thin and narrow, and only slightly broadened at its proximal end. An elongation of the process of metacarpus I is conspicuous; it probably serves as a weapon. Digit I is shorter than half the length of metacarpus II, and has a well-developed second phalange with a pointed, black claw. The characteristic peculiarities of the first phalange of digit II of the Limicolae are even more specialized here than in that group; the internal index process is large and the corner of the ulnar edge is elongated into a process. On the dorsal side of the basal phalange at the position of the ulnar process is another process—an elevation that reaches hook-like over the tendon of the M. inteross. palmaris and keeps this tendon from slipping off the bone when the wing is not completely opened. The second phalange of digit II is approximately as long as the first, the third is united with the second. Digit III is very snipe-like, somewhat curved toward the front, and lacks any process.

The wing muscles in *Chionis* (Fig. 26C, D, E) are more developed than in the Limicolae and one can appreciate immediately that the sheathbills must frequently use a hovering flight. The M. ext. metacarpi radialis is rather long with a short flattened tendon; the M. ext. pollicis longus is long and large with a short tendon which merges with that of the M. ext. metacarpi radialis before their joint insertion. The M. flex. metacarpi ulnaris is large and fleshy. The M. flex. carpi ulnaris is not very thick; its tendon comprises about one-fourth the entire length of the muscle. The Lig. humero-carpale is very well-developed and the M. flex. dig. sublimis is, therefore, small. The M. flex. dig. profundus is not very large, and extends over half the length of the lower arm. The tendons of both digital flexors insert on the second phalange of digit II.

The M. ext. dig. communis reaches to about the middle of the lower arm; its tendon curves sharply before insertion and is restrained at its curve by a well-developed loop of the Lig. digito-metacarpale (Fig. 26C). The M. abd. indicis is large, its tendon curves dorsally and covers the site of insertion of the tendon of the M. ext. dig. communis (Fig. 26E). The M. flex. dig. III is rather large and runs as a muscular ribbon over the entire length of

SYSTEMATIC OBSERVATIONS

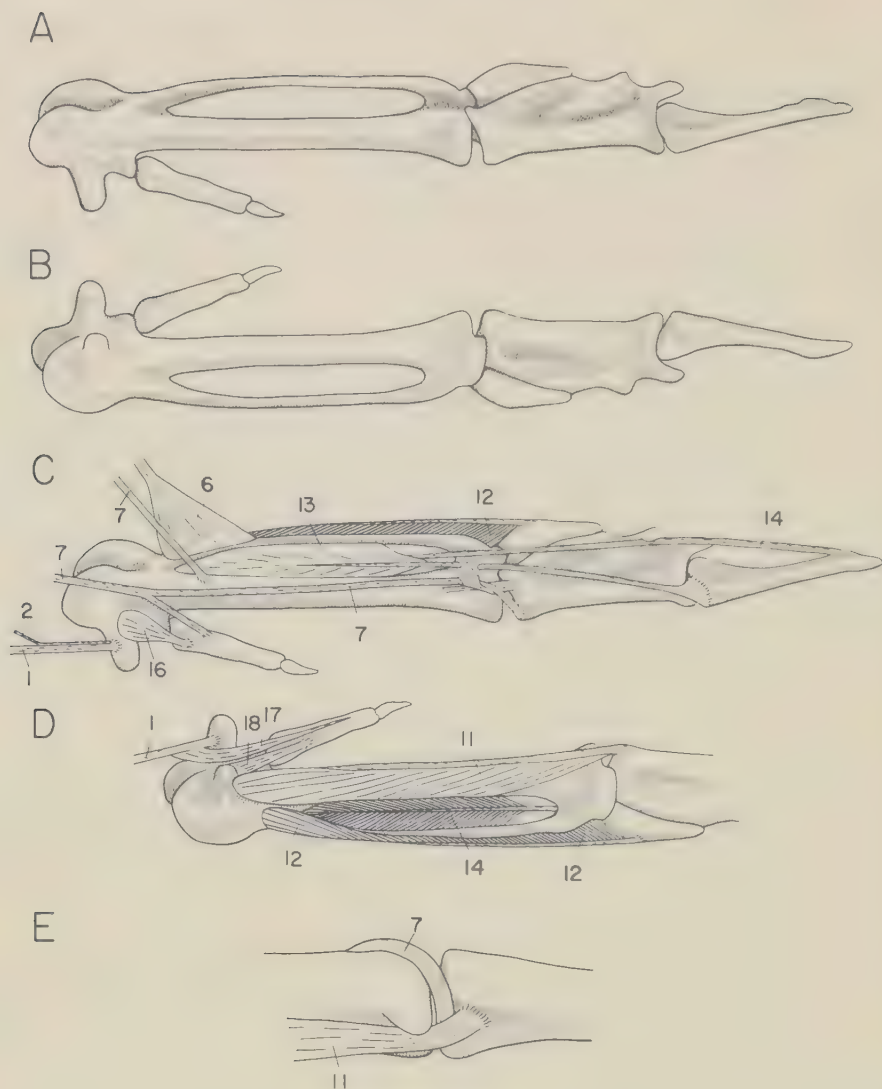


FIG. 26. Manus of *Chionis alba*. (A) Dorsum of the skeleton. (B) Venter of the same. (C) Dorsum of the musculature. (D) Venter of the same. (E) Radial view of metacarpus II.

metacarpus III. The *M. ulni-metacarpalis dorsalis* is small; it reaches only along the proximal third of metacarpus III. The *M. inteross. dorsalis* does not extend to the distal end of the intermetacarpal space; its tendon runs diagonally over the basal phalange of digit II. The *M. inteross. palmaris* is about as long, its tendon is strongly attached to the dorsal side of the first phalange of digit II. A complete set of muscles insert on the pollex. The *M. flex. pollicis* is small (Fig. 26D). The tendon of the *M. abd. pollicis* extends almost to the claw phalange of digit I.

CHARADRIIFORMES

Discussion.—One can say that *Chionis* belongs unquestionably to the Charadriiformes, but forms an aberrant group within the order. Its total appearance, and among other things particularly the morphology of its flight apparatus, makes it seem doubtful that the genus originally evolved under geographic conditions similar to those of the present habitat. Rather, one can assume that the ancestors of *Chionis* evolved under continental conditions and as terrestrial birds in open country. If one considers that today *Chionis* lives on isolated islands around the Antarctic and while that continent is ice-covered now, it had a moderate climate during the beginning of the Quaternary, then the possible place of origin of this bird is not difficult to surmise!

THINOCORIDAE

Introduction.—The seedsnipe are a small group of shorebirds consisting of two genera of two species each, which are distributed over the steepes and high mountain deserts of South America from the central Cordilleras to Tierra del Fuego. All species are terrestrial, run and fly rapidly, and can fly long distances. Their wing is of medium length with a compact point; it is, in general, what can be called a “rapid-flight wing”, but not one so highly specialized in this respect as that of the Limicolae. There are 10 primaries, with a tiny vestige of the 11th. The secondaries are diastataxic.

Species studied—*Attagis malouinus*.

Description.—The skeleton of the seedsnipe is massive, as its body is not compressed laterally as in the Limicolae (Fig. 27A, B). The arm portion of the wing is shorter, but the skeleton of the manus is narrow and like that in the Limicolae. Metacarpus II has a deep groove. Its distal process is turned ventrally, as in all Charadriiformes, but in addition a small process exists on the dorsal side of the metacarpus that assists in retaining the curve of the tendon of the M. ext. dig. communis (Fig. 27A, B). Metacarpus III is exactly like that in the Limicolae. Digit I is not long and lacks a second phalange. The basal phalange of digit II is more compact than the average one in the Limicolae, but it resembles the Limicolae phalange in its shape. The internal index process is well-developed. The second phalange of digit II is rather massive. Digit III is exactly the same as that in the Limicolae and completely lacks any process.

The muscles (Fig. 27C, D, E) are more developed than in the Limicolae, but not to the degree that one would expect to find in a terrestrial bird that has a strong wing-beat. The M. ext. poll. longus is short with a long, thin tendon that unites with the tendon of the M. ext. metacarpi radialis before their insertion. The M. flex. carpi ulnaris has a rather long tendon. The Lig. humero-carpale is well-developed; hence the M. flex. dig. sublimis is small and weak. Its tendon does not quite reach the second digit of digit II. The tendon of the M. flex. dig. profundus inserts on the second phalange of digit II and does not ossify. The M. flex. metacarpi ulnaris is large.

SYSTEMATIC OBSERVATIONS

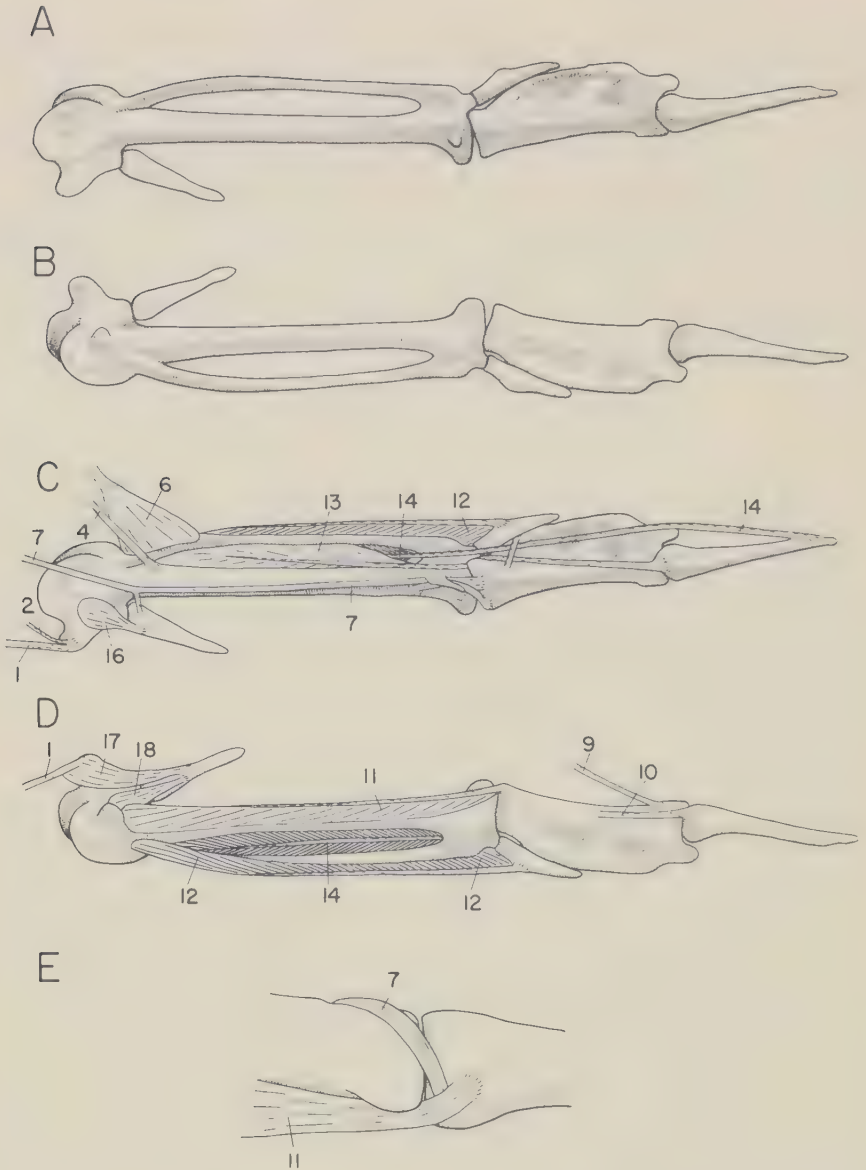


FIG. 27. Manus of *Attagis malouinus*. (A) Dorsum of the skeleton. (B) Venter of the same. (C) Dorsum of the musculature. (D) Venter of the same. (E) Radial view of metacarpus II.

Its tendon inserts on a small elevation on metacarpus II, which could be described as the beginning rudiment of the muscular tubercle.

The tendon of the M. ext. dig. communis curves sharply before insertion; it is held in place by a well-developed Lig. digito-metacarpale (Fig. 27C). The small process of metacarpus mentioned above also helps to fix the curve

CHARADRIIFORMES

of this tendon. The M. abd. indicis is large with a short tendon that curves dorsally before its insertion and covers the area of insertion of the tendon of the M. ext. dig. communis (Fig. 27E).

The M. flex. dig. III lies along the entire metacarpus III as a rather broad ribbon. The M. ulni-metacarpalis dorsalis, on the other hand, is very small and reaches, at the most, along the proximal quarter of metacarpus III. The M. inteross. dorsalis does not quite reach the distal end of the intermetacarpal space; its tendon extends diagonally over the basal phalange of digit II. The pinnate M. inteross. palmaris is as long as the previous muscle. All four muscles to digit I are normally developed. The tendon of the M. abd. pollicis reaches only up to the middle of the pollex.

Discussion.—From the anatomy of the wing it is clear that *Attagis* belongs to the Charadriiformes, but from the comparative evidence available it is impossible to determine the affinities of *Attagis* to the several subgroups of this order. The morphology of its wing is too neutral in this regard. In the external morphology of the wing, *Attagis* differs sharply from all Limicolae except *Chionis*.

The external structure of the wings of *Attagis* and *Chionis* is conspicuously similar, even though their habitats and ways of life are very different. If the morphology of the wings of *Attagis* and *Chionis* are compared one will find some of the shared resemblances are those characteristics that distinguish these birds from other Charadriiformes. In these features *Chionis* is clearly the more specialized, but in other respects it appears more primitive than *Attagis*. For example, *Chionis* has a well-developed claw phalange that no longer exists in *Attagis*.

Examining these birds and their affinities from a geographical point of view, the following remarks can be offered. The Thinocoridae are not closely related to any other members of the avifauna of South America. They are outsiders. This is particularly conspicuous since this group is so small. But, if one assumes that the Thinocoridae are the remanent of a formerly richer group that exists now only at the periphery of its once larger geographic range, then one may possibly conclude that the Thinocoridae and the Chionididae are remotely related, but nonetheless still more closely related to one another than to other charadriiforms.

LARI

The gull, terns, and their allies are a rather large group of birds of world-wide distribution that are all associated with water. All members can swim, but they secure their food mainly by "search-flights," for which they are particularly adapted. For overwater flight a bird must be able to overcome strong winds, for which the relatively narrow and pointed wings of the Lari are well suited. In their overall dimensions the Lari resemble the Limicolae, but they are considerably larger. True gliding flight is used only by the larger species but seldom while feeding. Usually Lari fly with slow, even wing beats; when they increase their speed the wings are held at a sharper angle.

SYSTEMATIC OBSERVATIONS

All members have 10 primaries, and a vestige of the 11th. This suborder contains four families.

STERCORARIIDAE

Introduction.—The skuas and jaegers live mainly near the oceans in the arctic, subarctic, and boreal zones; one species is distributed bipolarly. The stercorariids feed mainly by robbing other birds. Their flight is vigorous and they can make sudden shifts in speed and direction, and also accelerate rapidly. The shape of the wing varies according to size; the larger the species, the relatively broader the wing.

Species studied.—*Stercorarius longicaudus*, *S. parasiticus*, *S. skua*.

Description.—The arm portion of the wing is elongated in the Stercorariidae (Fig. 28A) as compared to the Limicolae; the lower arm is longer than the manus. The skeleton of the manus is very similar to that in the Limicolae, but longer. Digit I is considerably less than half the length of metacarpus II. It always has a second phalange with a small, but pointed claw (Fig. 28A). Digit II is somewhat shorter than the carpometacarpus. Its first phalange is perforated in two places, yet the fontanelles are small, irregular in shape, and vary individually. The internal index process is well-developed, and larger than in the Limicolae. The second phalange is long and bears on its tip a very small vestige of a third phalange, which may be absent in some individuals. Digit III is short, noticeably curved radially, pointed, and without processes.

The development of the muscles is also very similar to those of the Limicolae, but they are all weaker (Fig. 28B). The M. ext. metacarpi radialis is slender and much shorter than its tendon; the M. ext. poll. longus is short and small with a long thin tendon; and the M. flex. carpi ulnaris is also weak with a rather long tendon. Similarly short are the other muscles that originate from the lower arm. The Lig. humero-carpale forms a broad, strong band; the small weak M. flex. dig. sublimis originates from its inner side. The tendon of this muscle, as well as the one of the M. flex. dig. profundus, inserts on the second phalange of digit II. The tendon of the latter may ossify partly in the portion lying next to metacarpus II.

The tendon of the M. ext. dig. communis curves before its insertion, but only slightly, much like that in the Limicolae (Fig. 28C). The loop of the Lig. digito-metacarpale is well-developed, much more so than in the plovers, and more similar to that found in the higher Limicolae (Fig. 28B). The M. abd. indicis is large, its tendon curves dorsally before inserting, and it covers the site of insertion of the tendon of the M. ext. dig. communis. The M. ulni-metacarpalis dorsalis is small and spreads over only the basal quarter of metacarpus III, yet it is connected to digit III by means of a long, thin tendon. The M. flex. dig. III is rather large. It originates from the proximal end of metacarpus III and partly covers the dorsal surface of the distal end of the intermetacarpal space.

The pinnate, almost symmetrical, M. inteross. dorsalis almost reaches the

CHARADRIIFORMES

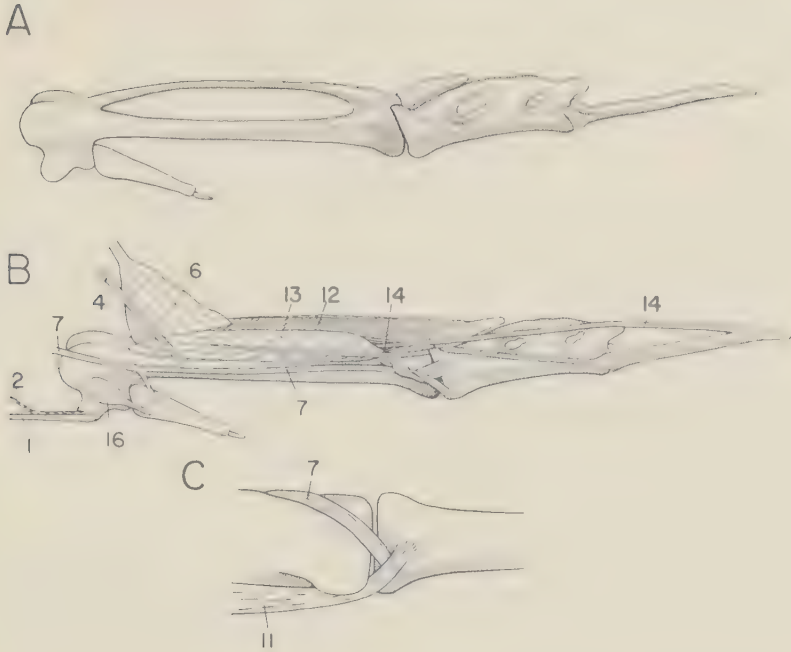


FIG. 28. Manus of *Stercorarius longicaudus*. (A) Dorsum of the skeleton. (B) Dorsum of the musculature. (C) Radial view of metacarpus II.

distal end of the intermetacarpal space. Its tendon runs diagonally over the dorsal side of the basal phalange of digit II in a deep groove. The *M. inteross. palmaris* is also pinnate and reaches the distal end of the intermetacarpal space. The course of the tendon of this muscle is determined by its attachment to the dorsal surface of the first phalange of digit II by strong connective tissue, not by a groove or channel in the bone. The tendon of the *M. abd. pollicis* almost reaches the second phalange of the pollex. A rather large vestige of the tendon of the *M. flex. dig. sublimis*, as well as a small vestige of the tendon of the *M. inteross. dorsalis*, are attached to the second phalange of digit II.

Discussion.—In general, the morphology of the wing of the Stercorariidae strongly resembles that of the Limicolae. The main differences (large skeleton, weak muscles) can be explained by the “search flight” specialization of the Stercorariidae. In their evolutionary development, however, the skuas have not reached a higher level than the Limicolae. The presence of a claw phalange on digit I, of tendon vestiges on the second phalange of digit II, of a tendon from the *M. abd. pollicis* that almost reaches the claw of the pollex, and of a slight curve in the tendon of the *M. ext. dig. communis*, all indicate a level of evolutionary development approximately corresponding to that of the Charadriidae. It appears that the Stercorariidae have specialized in “search flights”. This specialization had no influence on the “primitive”

SYSTEMATIC OBSERVATIONS

characters. But it is certain that the Stercorariidae branched from the charadriid lineage a long time ago and have evolved independently.

LARIDAE

Introduction.—The gulls are a group of about 45 species that are distributed over the entire world. Most species live in temperate and cold zones of the northern hemisphere. They are less numerous in the southern hemisphere and the smallest number of species occurs in the tropics. The true larids have specialized the economical “search flight” to a high degree, and they glide rather frequently. Since this family contains, in general, large species, the wings are rather broad (Stegmann, 1950). The wing tip is neither very long nor very pointed, but the arm portion is strongly elongated

Species studied.—*Larus ridibundus*, *L. canus*, *L. argentatus*, *Rhodostethia rosea*, *Pagophila alba*.

Description.—The skeleton of the wing is similar to that of the Stercorariidae, yet in the smallest forms, which have long primaries (*Larus ridibundus*, *Rhodostethia rosea*, *Xema sabini*), the manus may reach the length of the lower arm or even longer. A second phalange is always present on digit I, but it is smaller than that in the Stercorariidae (Fig. 29A, B). The third phalange on digit II is very small and regularly perforated in two places; the fontanelles are large and regular in shape. Digit III has no process and is curved toward the ulna.

In the structure of the muscles of the wing (Fig. 29B, C), the Laridae resemble strongly the Stercorariidae. All muscles are short with long tendons. The tendon of the M. ext. dig. communis curves less just before its insertion than that of the Stercorariidae. The loop of the Lig. digito-metacarpale is well-developed, but not all of the fibers of the ligament participate in the loop (Fig. 29A). The M. ulni-metacarpalis dorsalis is small. The M. inteross. dorsalis varies in length in the different species, but it never reaches the distal end of the intermetacarpal space. The muscles of digit I are normally developed. In *Pagophila*, the tendon of the M. abd. pollicis reaches the second phalange of digit I, in gulls of the genus *Larus* it is shorter, and in *Rhodostethia* it inserts on the proximal end of the basal phalange. In *Pagophila* the vestige of the tendon of the M. flex. dig. sublimis attaching to the second phalange of digit II is large and some of its fibers may connect across the articulation with the main, functional part of the tendon. In addition, a vestige of the tendon of the M. inteross. dorsalis attaches to the second phalange and, finally, a third tendon vestige, which probably belongs to the tendon of the M. ext. indicis longus, attaches to this bone. In other gulls this last vestige is missing and the other tendons are smaller than those in the Stercorariidae.

Discussion.—From the above description it can be seen that the gulls are very close to the Stercorariidae in their wing anatomy, but they are somewhat more advanced than the skuas. The fontanelles in the basal phalange

CHARADRIIFORMES

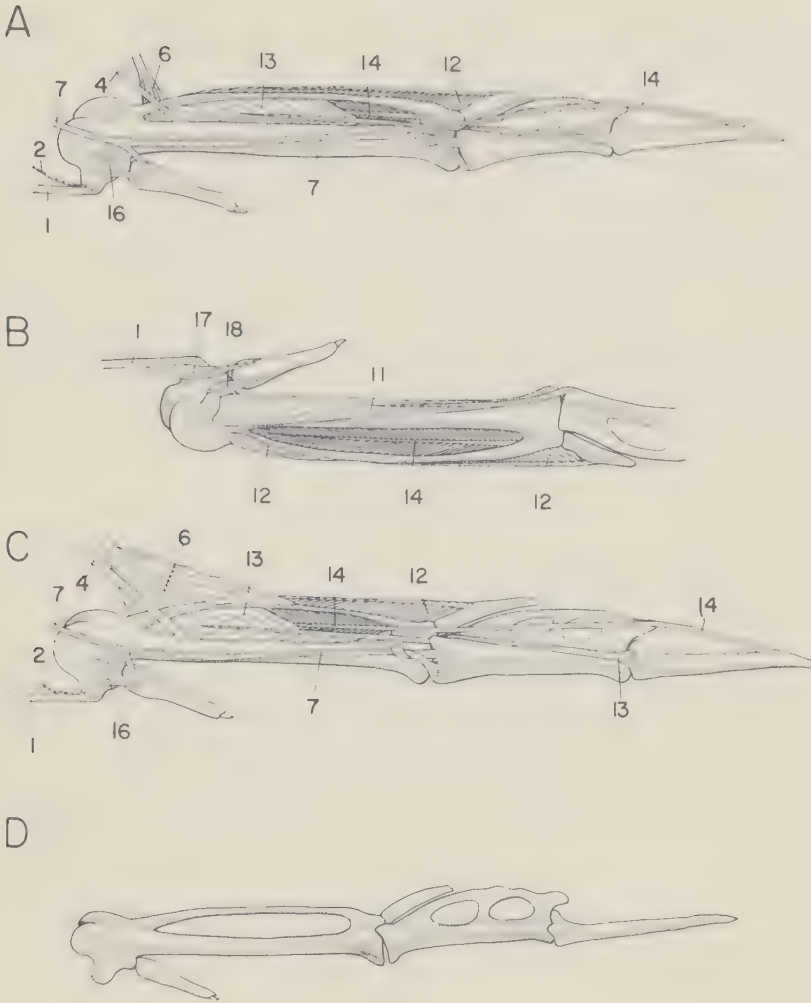


FIG. 29. (A) Dorsum of the manus of *Larus ridibundus* showing the musculature. (B) Venter of the same. (C) Dorsum of the manus of *Sterna hirundo* showing the musculature. (D) Dorsum of the skeleton of the manus of *Rynchops niger*.

of digit II are more strongly developed, the second phalange of the pollex is shortened, the tendon of the M. abd. pollicis is shorter, and the vestiges of the tendons attaching to the second phalange of digit II are smaller. *Pagophila* is, in these features, more primitive than the other gulls, but there is no reason to assume a closer relationship between *Pagophila* and the Stercorariidae.

STERNIDAE

Introduction.—The Sternidae contain almost as many species as the Laridae, but whereas the larids are least numerous in the tropics, the sternids have

SYSTEMATIC OBSERVATIONS

the greatest number of species distributed over the warmer areas of the globe. The terns are highly specialized in their way of flight. Most species are expert divers, diving into the water from the air; many of the small species live mainly on insects which are caught in flight. The wings of terns are long, narrow, and pointed. The distal part is especially long, while the arm portion is shortened in comparison to that of the Laridae.

Species studied.—*Sterna hirundo*, *S. paradisaea*, *S. albifrons*, *S. (Thalasseus) sandivicensis*, *S. (Hydroprogne) tschegrava (= caspica)*, *Chlidonias nigra*.

Description.—In all sternids the manus of the wing is longer than the lower arm, digit II is longer than the carpometacarpus, and the second phalange of digit II is longer than the first (Fig. 29C). The fontanelles are just as well-developed as in the Laridae and the internal index process is even longer than in the gulls. The claw phalange of the pollex is small, as in the Laridae, and it is often missing on digit II. Digit III is very similar to that in the larids, viz., without a process, pointed, and slightly curved.

The structure of the flight muscles is basically the same as in the Laridae, yet there are some peculiarities that characterize the Sternidae. The tendon of the M. ext. dig. communis is more sharply curved before the insertion than in the Laridae, and the loop of the Lig. digito-metacarpale is better developed (Fig. 29C). The M. ulni-metacarpalis dorsalis is very much larger than in the former groups; it is rather massive and reaches the middle of metacarpus III. The M. flex. dig. III is also large and partly covers the dorsal side of the intermetacarpal space. The tendons of the M. inteross. dorsalis and of the M. inteross. palmaris are fixed onto the dorsal surface of the basal phalange of digit II by bony elevations which may modify into channels.

The tendon of the M. abd. pollicis reaches the second phalange of digit I in *Chlidonias*, but is very short in the species of *Sterna* studied. Small vestiges of the tendons of the M. flex. dig. sublimis, the M. inteross. dorsalis, and sometimes the M. ext. indicis longus attach to the second phalange of digit II.

RYNCHOPIDAE

Introduction.—The skimmers are a small group of peculiar birds with a laterally compressed bill, with the knife-like lower mandible much longer than the upper. The three species are placed in a single genus and are distributed in the tropics of the Old and New World. The skimmers plow the surface of the water with the elongated lower bill and scoop fish from the surface of the water. For this feeding method the bird must fly low and, if possible, slowly, and with the least expenditure of energy. Hence, the wings do not beat below the body but are kept high in a peculiar and characteristic manner. Therefore, the Rynchopidae have even longer wings than the Sternidae, with an especially greatly elongated wing tip.

Species studied.—*Rynchops niger*.

CHARADRIIFORMES

Description.—The skeleton of the wing in the skimmer (Fig. 29D) is very similar to that of the Sternidae, but the internal index process is even longer which is in close agreement with the excessive length of the distal (10th) primary (Fig. 29C). The structure of the wing musculature is similar to that in the Sternidae. The M. flex. dig. III is so large that it partially covers the intermetacarpal space. But the M. ulni-metacarpalis dorsalis is considerably smaller than in the Sternidae. This might be associated with the fact that the Rynchopidae do not have to hover or rise vertically from their predominantly horizontal flight.

Discussion.—The three species of the genus *Rynchops* are generally very similar to each other. They are an aberrant group which undoubtedly branched off from the Sternidae at a time when the characteristic traits of the latter group were already evolved.

DISCUSSION

The gulls, terns, and their allies form a remarkably uniform and well defined group (Lari). The generally recognized subgroups (families) may be easily discerned by their wing morphology, yet the relationship between them is not always the same. The Stercorariidae are undoubtedly the most primitive and the Laridae are most advanced in their evolution. The Sternidae have retained some ancient characters in spite of their high degree of specialization, so that they cannot be considered, in any way, to have descended from the present-day Laridae. But the Rynchopidae may well be regarded as an aberrant group of the Sternidae.

To conclude, the Lari undoubtedly belong to the Charadriiformes. But a number of peculiarities place them (especially the Stercorariidae) no higher than the most primitive members of the order. Thus it may be concluded that the Lari have branched from the Charadrii at a time when the latter group had not yet attained its present morphological characteristics.

ALCAE

ALCIDAE

Introduction.—The Alcidae, which is the only family in this suborder, consists of an unique group of 12 genera and 22 species that dwells in the inshore waters of arctic and subarctic oceans. They dive and swim underwater with the help of their wings. All species are able to fly rapidly with very quick wing beats, but are not very agile and they are neither able to take-off steeply nor alight vertically. The wings are small, very narrow, and pointed with very hard and stiff wing feathers. One must remember that these minute wings are adaptations for "wing-swimming" locomotion. As already mentioned, such wings are disadvantageous for flight. It should also be added that because the wing is narrow it is forced to assume a peculiar posture when the bird is flying horizontally. Of course, in horizontal flight the center

SYSTEMATIC OBSERVATIONS

of gravity of the bird has to be on a plane that connects the force points of both wings. It is clear that with relatively different widths of the wings, this ratio can only be obtained by a difference in the position of the wing. In broad-winged species the wings have to be strongly spread out and pushed cranially, but in narrow-winged birds the hand portion must not be completely spread. However, in the alcids the wings are so narrow and small that they cannot sustain the balance necessary for horizontal flight if they are handled in this manner. The entire wing, therefore, has to be pushed caudally and this is achieved in a most interesting manner (Stegmann, 1949). In these birds the upper arm is only slightly spread away from the body in horizontal flight. That is to say, flight is achieved with the elbow joint pressed against the body. Hence the wing is shifted backward for almost the whole length of the humerus and appears as if it were fastened to the middle of the body instead of to the shoulder joint. The wing has 10 primaries and a vestige of the 11th. The secondaries are arranged diastataxically, with a tendency toward a transition to a eutaxic condition (Steiner, 1918).

Species studied.—*Alle alle*, *Uria aalge*, *Cephus grylle*, *Aethia cristatella*, *Aethia pusilla*, *Cyclorhynchus psittacula*, *Fratercula arctica*.

Description.—The skeleton of the wing is very shortened (Fig. 30A). The lower arm is shortest while the manus is longest. Digit I has a well-developed, but rather small, claw phalange. The third phalange of digit II is rudimentary and may be missing in some individuals (Fig. 30A). The pollex is long and more than half the length of metacarpus II. A large alula is very noticeable in the extremely small-winged alcids; this helps to increase the lifting force (Stolpe and Zimmer, 1938), which is especially important during take-off and landing. The basal phalange of digit II is narrower than in the Lari and its plate is massive and not perforated. It has a small internal index process. Digit III is hardly curved, but is otherwise like that in the gulls, namely pointed and without any process.

The arrangement of the wing muscles is similar to that of the sandpipers and snipes, but because the skeleton is shortened all muscles appear to be more massive (Fig. 30C,D). The muscle part of the M. ext. metacarpi radialis is not shorter than its tendon. The M. ext. poll. longus is larger than that in the plovers and gulls. The M. flex. carpi ulnaris is thick and fleshy with a very short tendon. The Lig. humero-carpale is well-developed, but the M. flex. dig. sublimis is not small, as is usual, as it arises from the whole inner surface of the ligament. The tendons of the M. flex. dig. sublimis and of the M. flex. dig. profundus insert on the second phalange of digit II. The M. flex. metacarpi ulnaris is unusually large. This may be associated with the fact that underwater swimming is achieved through strongly bent wings which are in a position where the M. flex. metacarpi ulnaris can best develop its force. Therefore, it was not necessary for the muscular tubercle to evolve in the alcids and the M. ulni-metacarpalis dorsalis could remain small. The M. flex. dig. III is large in the alcids. It runs along the entire

CHARADRIIFORMES

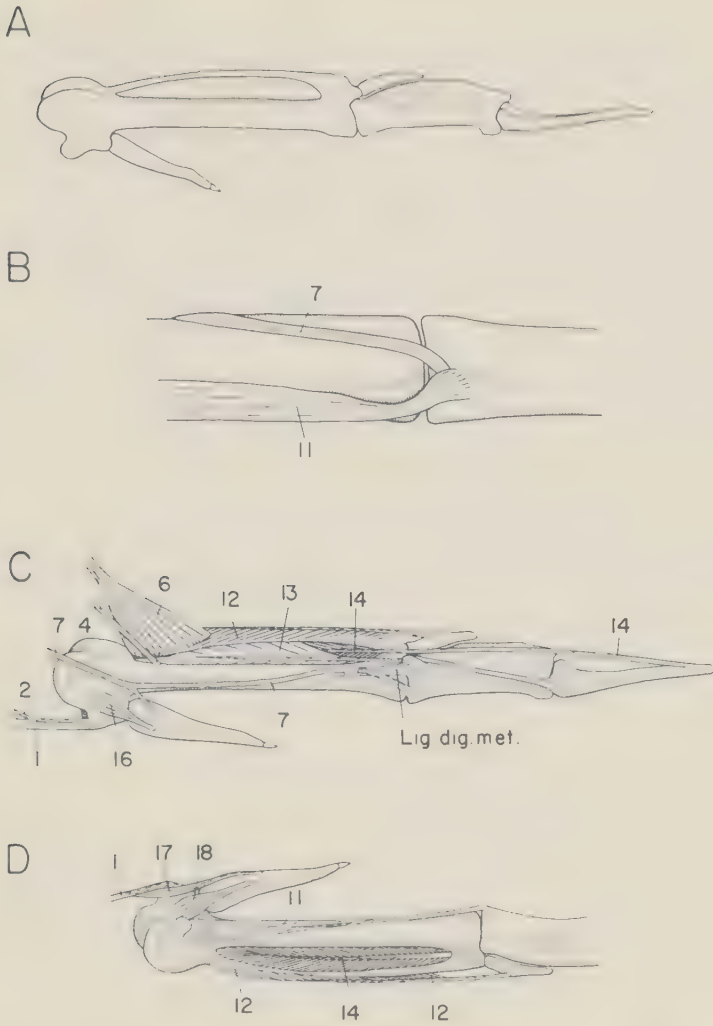


FIG. 30. (A) Dorsum of the skeleton of the manus of *Aethia cristatella*. (B) Radial view of metacarpus II of *Aethia cristatella*. (C) Dorsum of the manus of *Cepphus grylle* showing the musculature. (D) Venter of the same.

metacarpus III and partly covers the dorsal side of the intermetacarpal space (Fig. 30C,D).

The course of the tendon of the M. ext. dig. communis is very strange in the auks; it curves very gradually so that digit II is weakly supinated by its pull (Fig. 30C). There is a Lig. digito-metacarpale, but it runs along next to the tendon of the above muscle without having any influence on its direction. The tendon is surrounded by strong connective tissue which is attached to metacarpus II. The distal process of metacarpus II does not take part in the retention of the tendon in its curved position, since the

SYSTEMATIC OBSERVATIONS

process is turned ventrally and the tendon of the M. abd. indicis glides over it at its curve (Fig. 30B), as is characteristic of all Charadriiformes.

The pinnate M. inteross. dorsalis reaches the distal end of the intermetacarpal space. The M. inteross. palmaris is equally long. The four muscles of the pollex are normally developed. The tendon of the M. abd. pollicis reaches at least to the middle of digit I, and in some species it reaches the second phalange (Fig. 30D). There are vestiges of the tendons of the M. flex. dig. sublimis and of the M. inteross. dorsalis, and in some species also of the M. ext. indicis longus, attached to the second phalange of digit II.

Discussion.—From the above description it can be seen that the Alcidae are, in spite of their biological and morphological peculiarities, closely related to the Limicolae and the Lari. The presence of a series of primitive characters in the alcids makes it probable that they represent a group which has evolved independently for a long time, whose rank is equal to that of the Limicolae and the Lari. The prototype of the auks might have been closest biologically to the early Limicolae, which at that time had moderately long and narrow wings. It is from these long- and narrow-winged birds that the modern Limicolae, with their "hurried flight" wing, evolved and, as side branches, the Lari with their large wings adapted for searching flight on the one hand and, on the other, the alcids with their small wings adapted for underwater swimming.

DISCUSSION

The Charadriiformes follow closely the Gruiformes and are, in general, more highly evolved than the latter. One can see clearly an evolutionary series in the Rallidae, Otidae, and Gruidae, in which the Rallidae are very primitive and the Gruidae reach approximately the same evolutionary level as the Limicolae. Evolution in the Charadriiformes, in contrast, was a radiation from the primitive stock in several different directions.

COLUMBIFORMES

The pigeons, doves, and their allies, a large group of birds with a world-wide distribution, are undoubtedly closely related to the Charadriiformes. Gadow (1891–1893) place this group within his great order of Charadriiformes. However, he allowed for the possibility that the pigeons and the sandgrouse (the Pteroclididae of the suborder Pterocletes) form a separate group, which could be contrasted with the other Charadriiformes by separating the order into two groups of equal ranking (suborders or a higher ranking), viz., the Laro-Limicolae and the Pteroclo-Columbae. This important insight into the relationships within the charadriiform-columbiform complex is still valid, but modern systematists prefer to elevate each of the two groups to the rank of an order. Thus, it is quite legitimate to consider the Charadriiformes and the Columbiformes (e.g., in the sense of Wetmore, 1960) as two separate orders, if together they are placed within the superorder Charadriomorphae.

COLUMBIFORMES

But one must not forget that the Laro-Limicolae and the Pteroclo Columbae are more closely related to each other than to all other birds.

The pigeon-like birds differ from the plover-like birds in that (1) they are adapted to a vegetarian diet and (2) they are highly adapted to "hover flight." These two characteristics have caused structural changes in the entire body. Thus a distinct avian form evolved that is clearly characterized morphologically and all representatives of which can be recognized at a glance. The Columbae and the Pterocletes are today usually recognized as two different suborders, but it is clear that the differences between the two groups are smaller than those between the pigeon-like birds and the plovers and their allies (Charadrii, Lari, and Alcae). Nevertheless, the Columbidae and the Pteroclididae are well-characterized and intermediates between them are unknown.

COLUMBIDAE

Introduction.—The pigeons and doves together constitute the largest number of species in the Columbiformes. They are distributed over the entire world with the exception of the arctic and antarctic. The birds belonging to this family can be assigned easily to the charadriomorph birds on the basis of the structure of their bill, with the exception, of course, of a few aberrant forms. They live mainly in forests and rocky areas, which has resulted in a restructuring of their feet. Their habit of flying long distances for food necessitates a "hurrying wing" ("Eilflugel"), which in the case of the pigeons has been inherited from the plovers with some modifications (Stegmann, 1969).

The characteristic breeding sites of pigeons are trees and cliffs which means that a very maneuverable flight is necessary. This is achieved through the highly developed abilities of hovering in one place and of propulsion hovering (Lorenz, 1933). All morphological characteristics of the flight apparatus in the columbids can be explained as adaptations to these methods of flight. The pigeon wing is of moderate length with a rather short arm portion and very stiff, hard feathers. It is moderately broad and pointed. Pigeons have 10 primaries, and a vestige of the 11th. The secondaries in most species are diastataxic, but in some short-winged forest forms they are eutaxic.

Species studied.—*Columba livia*, *C. eversmanni*, *C. palumbus*, *Streptopelia orientalis*, *S. turtur*, *S. decaocto*, *Treron calva*, *Ducula aenea*, *D. chalconota*, *Goura cristata*, *Didunculus strigirostris*.

Description.—The wing skeleton in the Columbidae is relatively short, compact, and heavy-boned (Fig. 31A,B). The carpometacarpus is longer than the lower arm. Digit II is about as long as metacarpus II and the second phalange of digit II is longer than the basal one. The groove in metacarpus II for the tendon of the M. ext. dig. communis is poorly developed, but at the distal end of this bone there are two very conspicuous elevations that serve as guides for the tendon. The free ends of these bony projections are usually joined by fibrous connective tissue (Fig. 31A). Metacarpus III

SYSTEMATIC OBSERVATIONS

is rather broad, flat and twisted so that at the proximal end the outer surface faces more or less ventrally and at the distal part it faces backward toward the ulna. Digit I is short with a very small vestige of a second phalange, which is lacking in many species. The basal phalange of digit II is broad, massive, and with well-developed sculpture on its dorsal surface. The internal index process is strongly developed and larger than that in gulls and terns. The second phalange of digit II is not only long, but also very broad. Digit III is moderately long, laterally compressed, and has a large pointed process. In this respect the Columbidae are very different from the Charadriidae. A similar process occurs on digit III in the Gruiformes, but it is not so large as that in the Columbidae.

The wing muscles in the Columbidae are much more massive (Fig. 32A, B, C, D, E) and stronger than in any Charadriiformes. In the lower arm all muscles are long with short tendons. Even in the *M. ext. metacarpi radialis* the muscular part is at least twice as long as the tendon. The *M. ext. poll. longus* is unusually long. It runs as a rather broad ribbon along the entire radius and has a short tendon. This tendon is flat, ribbon-shaped, and inserts beneath the tendon of the *M. ext. metacarpi radialis* without uniting with the latter tendon before their insertions. The *M. ext. dig. communis* occupies about three-fourths of the length of the lower arm. The *M. flex. metacarpi ulnaris* extends over the entire length of the lower arm and has an especially strong aponeurotic tendon, which pulls it toward the ulna. This is, indeed, necessary because, in the Columbidae the ulna is strongly curved and the muscles occupying the inner side of the curve is therefore also curved.

The *M. flex. carpi ulnaris* is very thick and fleshy. It extends as a mass up to its site of insertion on the ulnare carpale. The *Lig. humero-carpale* is well-developed, as in the Charadriiformes, but the *M. flex. dig. sublimis* is also large. It originates from the inner side of the ligament, as in the Charadriiformes, but it is long and fleshy. The *M. flex. dig. profundus* runs

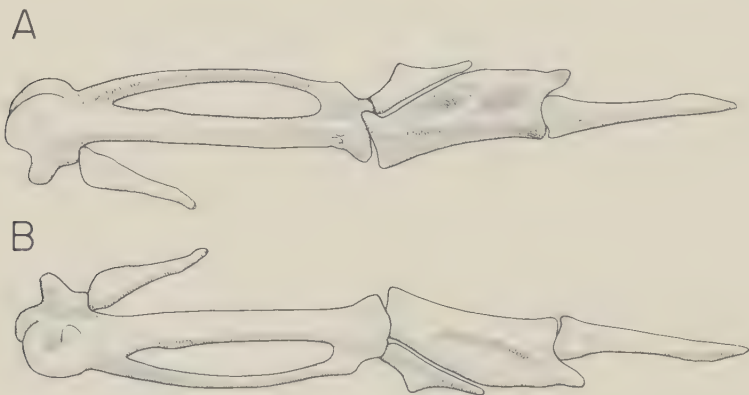


FIG. 31. Manus of *Columba livia*. (A) Dorsum of the skeleton. (B) Venter of the same.

COLUMBIFORMES

along the entire length of the lower arm, and even covers the M. ulni-metacarpalis ventralis. The tendons of the M. flex. dig. sublimis and of the M. flex. dig. profundus insert on the second phalange of digit II.

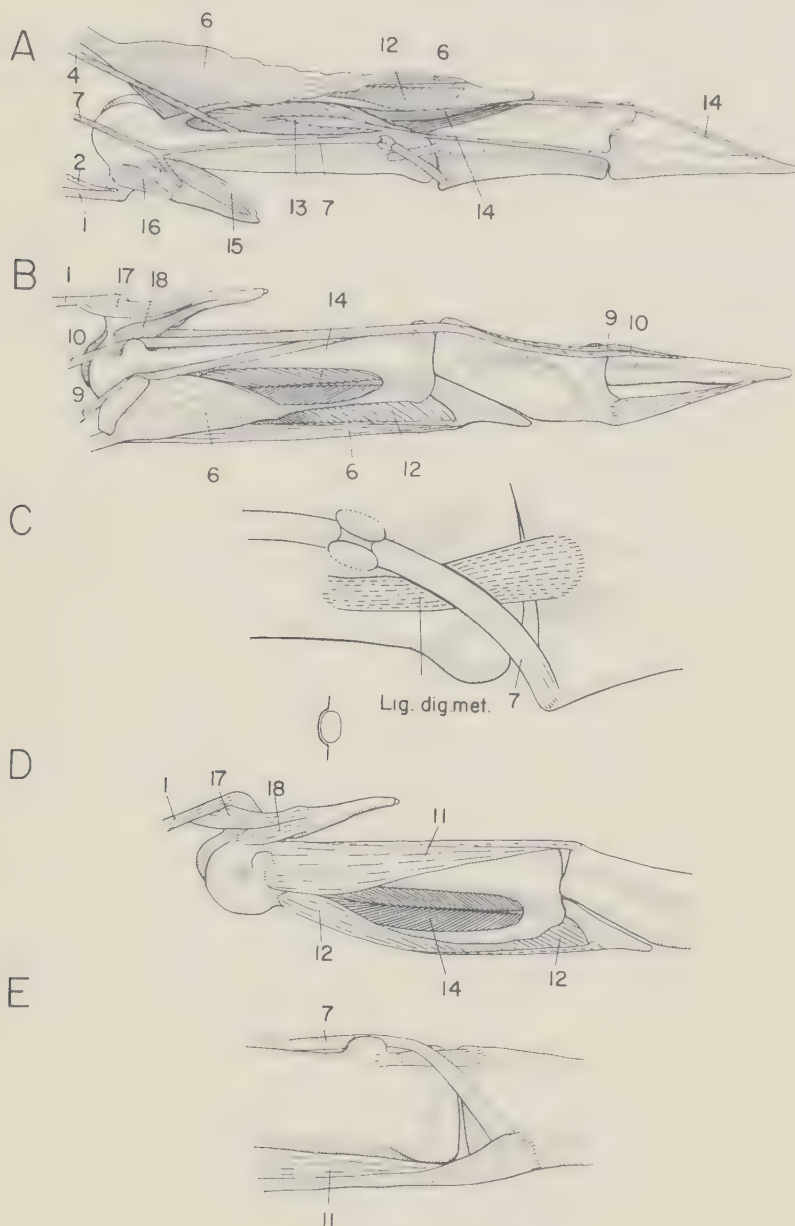


FIG. 32. Manus of *Columba eversmanni*. (A) Dorsum of the musculature. (B) Venter of the superficial musculature layer. (C) Apparatus for restraining the curve of the tendon of the M. ext. dig. communis. (D) Venter of the deep musculature layer. (E) Radial view of metacarpus II.

SYSTEMATIC OBSERVATIONS

The tendon of the *M. ext. dig. communis* lies rather openly on the surface of metacarpus II. It is bound to the bone at its distal end only with the assistance of the two previously mentioned elevations between which the tendon passes (Fig. 32A). It continues as a flat arc toward its site of insertion on the anterior (radial) side of digit II (Fig. 32E). The columbids have a *Lig. digito-metacarpale*, but it does not take part in restraining the tendon of the *M. ext. dig. communis*. The tendon crosses the ligamentous band only after it has taken its new direction with the help of the channel on the distal end of metacarpus II. The *Lig. digito-metacarpale* is deeply indented at the point of crossing with the tendon, but shows no tendency to encircle the tendon with any part of its fibers forming a loop (Fig. 32C). Moreover, there is no need for such a loop because the Columbidae have another, unique method of restraining the tendon in order to alter its direction. The distal process is closer to the ventral than the dorsal side of metacarpus II. But, the tendon of the very large *M. abd. indicis* does not curve dorsally before its insertion, so that contraction of this muscle only abducts digit II without pronating it (Fig. 32D,E). The tendon of the *M. abd. indicis* covers the site of insertion of the tendon of the *M. ext. dig. communis*, as is characteristic of the Charadriiformes.

A characteristic peculiarity of the Columbidae is the extremely strong development of a ligament which I propose to call the *Lig. spirale*. In birds of many different groups there is a ligament that usually originates from the tendon of the *M. ext. indicis longus* at the proximal part of metacarpus II. From here it spirals around the bone and inserts on digit II under the tendon of the *M. abd. indicis*. It is of varying size and strength, or it may be entirely absent. In the Columbidae this ligament originates from the sheath of the tendon of the *M. ext. indicis longus* at the distal end of the ulna. It extends as a broad band to the site of insertion of the tendon of the *M. abd. indicis*, while a branch of the ligament extends past the basal phalange of digit II and inserts together with the tendon of the *M. inteross. dorsalis* on the second phalange of digit II. When the articulation of the hand is stretched (the hand extended on the lower arm), this ligament tightens and automatically contributes to the abduction of both phalanges of digit II. This peculiar apparatus for stretching digit II has not evolved in other birds.

The *M. ulni-metacarpalis dorsalis* is extremely strongly developed (Fig. 32A,B). It partially covers the ventral side of the intermetacarpal space, and in some species also covers the dorsal side of this space. It extends as a muscular band up to digit III and inserts on the process of this digit. The *M. flex. dig. III* is also large. It arises from the proximal end of metacarpus III, is fleshy, and may partly cover the dorsal side of the intermetacarpal space. This muscle is, in turn, extensively covered by the *M. ulni-metacarpalis dorsalis*. The tendon of the pinnate *M. inteross. dorsalis* is broadened within the muscle. The *M. inteross. palmaris* is very long, crosses to the dorsal side of the carpometacarpus at the distal end of the intermetacarpal space, and reaches almost to the tip of digit III. The muscles of the pollex are normally developed. There is a *M. flex. pollicis*. The *M. abd. pollicis* is

COLUMBIFORMES

rather large but its tendon falls well short of the proximal tip of digit I. No vestiges of any tendons are found on the second phalange of digit II.

Within the large family of columbids there are almost no observable differences in the morphology of the wing. The species studied within the genera *Columba* and *Streptopelia* can be differentiated only by their dimensions. The subfamily Duculinae is also very similar to the Columbinae in its wing anatomy. It appears that the skeleton of the manus is somewhat weaker in the small African species *Treron calva*, but the structure of its muscles resembles that of the larger columbines. In large *Ducula chalconota* and *D. aenea* the skeleton of the manus is, however, especially massive. Again the structure of the muscles is like that in the columbine pigeons; only a small difference in the method of restraining the tendon of the M. ext. dig. communis can be observed. The bony elevations, through which the tendon passes, are less developed and the Lig. digito-metacarpale shows some tendency to form a loop. One gets the impression that in these species the characteristic features of the Columbidae have not reached as high a degree of development as in the columbine pigeons. It is of special interest that the wing morphology of the very large Crowned Pigeon (*Goura cristata*) does not differ in any way from that of other pigeons. Moreover, the very aberrant species *Didunculus strigirostris* is typically columbid in its wing morphology, and the wing skeleton in the ground-dwelling, plover-like *Otidiphaps nobilis* is also very pigeon-like. Thus, one concludes that the Columbidae are highly uniform in the morphology of their wing.

Discussion.—I have already commented somewhat on the relationships between the Columbidae and the Charadriiformes. The description of the columbid wing morphology shows that the characteristics of the pigeons are generally adaptations to their highly specialized hovering flight. Only the peculiar apparatus for restraining the tendon of the M. ext. dig. communis at its arc cannot be explained as a hover-flight adaptation. However, if one considers that in the most primitive of the modern Charadriiformes, the plovers (Charadriinae), the loop of the Lig. digito-metacarpale is still in the beginning stages of its evolutionary development, one may assume that in their ancestors this restraining apparatus was not yet present. After the pigeons branched off from this ancestral lineage they could have evolved their own apparatus for the retention of the tendon of the M. ext. dig. communis.

PTEROCLIDIDAE

Introduction.—The sandgrouse are a small group of birds, of three genera and 16 species, that is distributed over the savannas and deserts of the Old World. They are truly terrestrial and cannot perch in trees. But in their general appearance, as well as in their locomotion, the sandgrouse show great similarity to the pigeons from which they have branched off as an aberrant group (Stegmann, 1969). Because they live in open country, they can sacrifice great maneuverability of flight in favor of acquiring higher speeds. Their wings are of an aberrant type because they have a thick cross section at

SYSTEMATIC OBSERVATIONS

the junction between the secondaries and the primaries, but the sandgrouse wing can be derived from that of the pigeons without difficulties. They have 10 primaries, with a tiny vestige of the 11th. The secondaries are diastataxic.

Species studied.—*Pterocles orientalis*, *P. alchata*, *Syrrhaptes paradoxus*, *S. (Tschang-tania) tibetanus*.

Description.—The skeleton of the wing of the Pteroclididae is very similar to that of the Columbidae (Fig. 33A,B). It is as compact and massive as that of the pigeons with the upper and lower arms short and the manus longer than either. The carpometacarpus is like that in the pigeons, but the groove for the tendon of the *M. ext. dig. communis* is better developed, while the two elevations on the distal end of the bone are relatively flat. The beginning rudiment of the muscular tubercle is present (Fig. 33B). Metacarpus III has the same configuration as that in the Columbidae, but is narrower. Digit I always has a very small second phalange. The first phalange of digit II is very pigeon-like but with a large internal index process that is generally longer than the process in the columbids. The second phalange is even more elongated than that of the pigeons. A third phalange exists only as the smallest vestige, or is completely gone. Digit III is also pigeon-like, but longer and with a smaller process.

The wing muscles are also like those of the pigeons (Fig. 33C,D,E), being strongly developed and generally long with a short tendon. The lower arm is fleshy and thick, as in the pigeons, and different from the characteristic configuration seen in the Limicolae. The *M. ext. metacarpi radialis* is enormously developed. Its tendon is short and flattened. The *M. ext. poll. longus* is equally long, just like that of the Columbidae. Most of the other muscles are extremely similar in morphology to those of the pigeons (Fig. 33D,C,E). Moreover the peculiar ligament—the *Lig. spirale*—with its several branches exists in the sandgrouse, exactly as in the pigeons. This characteristic ligament exists only in these two groups of birds.

Differences between Pteroclididae and the Columbidae can be found in the wing musculature as follows. The *M. flex. dig. sublimis* is smaller than that in the Columbidae. It originates from the inner side of the *Lig. humero-carpale* and is equally long in the Pteroclididae and the Columbidae, but is flatter in the latter taxon. The *M. ulni-metacarpalis dorsalis*, although fleshy and thick, is much shorter in the Pteroclididae than in the Columbidae, and reaches only up to the middle of metacarpus III. The *M. inteross. palmaris* is also shorter. It reaches the dorsal surface of the carpometacarpus through the distal end of the intermetacarpal space, but does not extend as far as the muscle in the Columbidae. All of these characteristics of the sandgrouse represent quantitative differences from the features present in pigeons and are, therefore, of minor importance.

A greater difference exists between the sandgrouse and the pigeons in the structure of the apparatus for supination of digit II. As mentioned, this apparatus is unique to the Columbidae. In the Pteroclididae the supinatory mechanism consists of the ordinary loop of the *Lig. digito-metacarpale*, as

COLUMBIFORMES

is present in many other groups of birds, including the Gruiformes and the Charadriiformes. This loop is very well-developed in the Pteroclididae, as all fibers of the Lig. digito-metacarpale take part in it (Fig. 33A).

Discussion.—Because the Columbidae and the Pteroclididae are very similar to each other in the general morphology of their wings, one cannot doubt

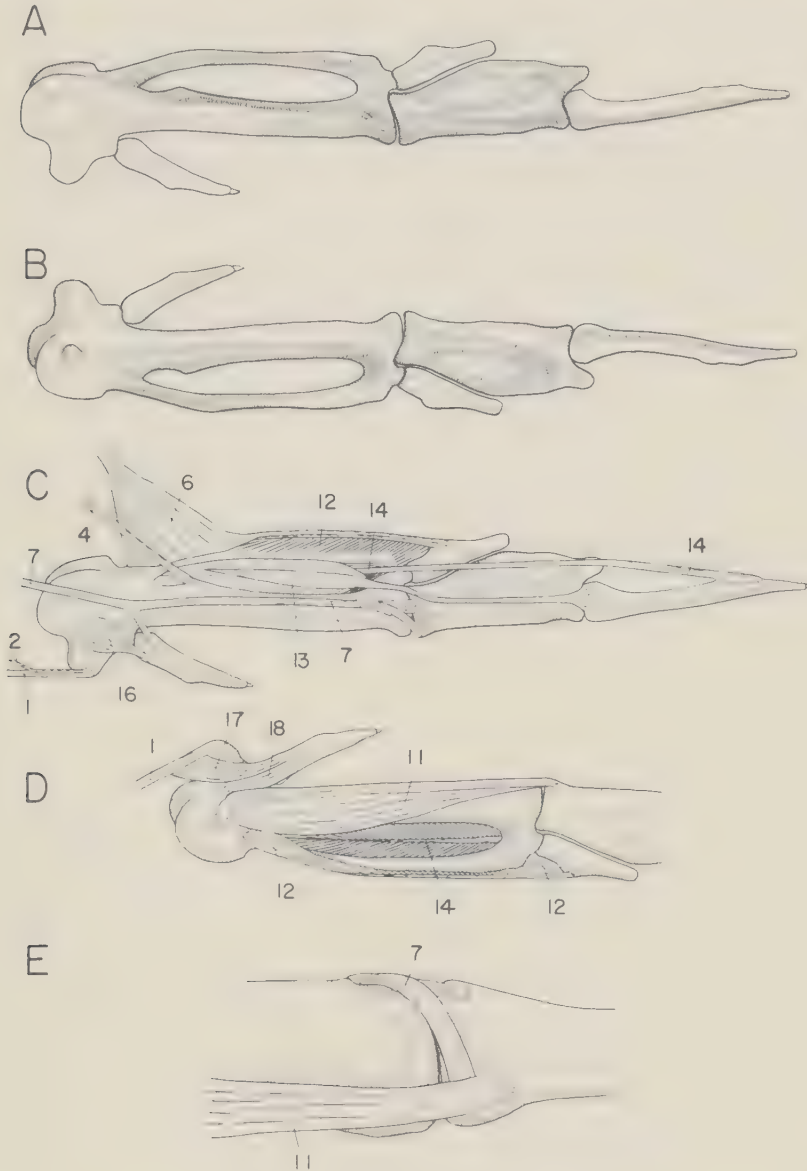


FIG. 33. Manus of *Pterocles orientalis*. (A) Dorsum of the skeleton. (B) Venter of the same. (C) Dorsum of the musculature. (D) Venter of the same. (E) Radial view of metacarpus II.

SYSTEMATIC OBSERVATIONS

that they are closely related. Thus, it is important to ascertain how these two groups evolved such different supinatory mechanisms of digit II, which is a rather critical aspect of their wing morphology. Because the function of the two features is the same in spite of their morphological differences, it is impossible that one supinatory mechanism could have evolved from the other. Their evolutionary origins must have occurred independently of one another from an ancestral group lacking such a mechanism. We have seen that within the Gruiformes and the Charadriiformes the loop of the Lig. digito-metacarpale evolved independently several times. Early stages in the evolution of this structure is found in the Rallidae, the true plovers, and the alcids. The origin of this feature, therefore, cannot be very old phylogenetically. The loop of the Lig. digito-metacarpale could have developed several times in different groups as an adaptation of the flight apparatus. But there were also several different morphological possibilities to restrain the M. ext. dig. communis in its curve, each of which could have evolved as an adaptation under the action of selection favoring the evolution of the loop of the Lig. digito-metacarpale. One of these possibilities occurred in the evolution of the Columbidae, giving rise to the groove and paired elevations at the distal end of metacarpus II.

Therefore, one can only assume that the Columbidae and the Pteroclididae descended from a common ancestor in which an apparatus for restraining the tendon of the M. ext. dig. communis had not yet developed, although the general morphological characters of the Pteroclo-Columbae complex had already evolved. It is very likely that the ancestors of this complex branched off the main stem of the Limicolae earlier than did the lineages leading to the Lari and to the Alcae.

DISCUSSION

The superorder Charadriomorphae (Charadriiformes and Columbiformes) exhibits a continuous series of groups starting with very primitive forms and gradually become more advanced to terminate with relatively highly specialized groups. It is not implied that one group evolved directly from the other, but that the general course of evolutionary change is clearly discernible. Among the Gruiformes, the Rallidae are very primitive, followed by the Otididae and other smaller groups, and ending with the highly evolved Gruidae. The Charadriiformes contain several suborders, which descending from a common ancestor, have radiated broadly in a fan shape. In general this order is more highly evolved than the previous one. The Columbiformes are descended from primitive ancestors of the Charadriiformes, but have evolved independently and have, at present, reached a higher evolutionary stage than all other groups of this large superorder. At the same time the Columbiformes comprise an end branch of this complex and are, so to speak, at the pinnacle of this group and not related to any descendent group.

PSITTACIFORMES

PSITTACIFORMES

Introduction.—The parrots are a large, isolated group of more than 300 species that inhabits tropical forests of all continents, but some species reach the northern and southern temperate zones. The peculiar and highly specialized form of the bill is associated with such an extreme change in the structure of the skull and jaw muscles, that one cannot reach any conclusions about the possible relationships of the parrots based upon comparative anatomical investigations of this part of the body. The feet are also highly specialized but it is now concluded that the zygodactyle arrangement of the toes has evolved independently in the several groups (Bock and Miller, 1959). It is, therefore, of special interest to examine the morphology of the wing of representative parrots. Since the flight ability of parrots is not particularly specialized, one can hope to find here some clues to the phylogenetic affinities of parrots.

Generally parrots feed on seeds with hard shells, such as nuts, for which they frequently have to fly long distances. Therefore, they need to be able to fly rapidly and far. On the other hand, because of the peculiar specialization of their feet, parrots can only climb about on branches and cannot jump from one branch to another, which means they also must be able to fly in the forest canopy. Thus, flight must be as agile and maneuverable as possible. These contrasting kinds of flight are similar to the situation in the pigeons (Stegmann, 1964, 1969). Agile flight can be achieved by a narrow, pointed wing, while maneuverable flight is attained through a highly developed ability to hover. The latter is independent of the shape of the wing, but requires strong flight muscles, especially the up-beat muscles.

In parrots, the wing is usually narrow and pointed or at least with a closed tip. Only the cockatoos and *Probosciger* have broad, rounded wings with well-developed propulsion feathers. The arm portion of the wing is of medium length, elongated in the larger and shortened in the smallest birds. Parrots have 10 primaries, without a vestige of the 11th. The secondaries are diastataxic.

Species studied.—*Strigops habroptilus*, *Nestor notabilis*, *Lorius garrulus*, *Probosciger aterrimus*, *Cacatua galerita*, *C. sulphurea*, *Ara ararauna*, *A. macao*, *Bolborhynchus lineola*, *Brotogeris tirica*, *Pionus menstruus*, *Amazona aestiva*, *Poicephalus robustus*, *Psittacus erithacus*, *Psittacula krameri*, *Psittacula alexandri*, *Agapornis roseicollis*, *Eclectus roratus*.

Discussion.—Gadow (1891–1893) combined the parrots and the cuckoos into one order. This arrangement was accepted for a long time but Steiner (1918), based on his studies of eutaxy and diastataxy, concluded that the cuckoos and the parrots did not fit together. In Peters (1937) and Wetmore (1960) the Psittaciformes are placed between the Columbiformes and the Cuculiformes, followed by the Strigiformes. Therefore, it is necessary to first make a comparison of the parrots with the cuckoos and, secondly, with the pigeons.

SYSTEMATIC OBSERVATIONS

At the first glance it is clear that the skeleton of the manus of the parrots (Figs. 34A, B, 37A, B) shares no basic similarities with that of the Cuculidae and the Musophagidae. In some respects more similarities exist between the hand skeleton of the parrots and that of the pigeons, but here too there are some differences. The carpometacarpus of the parrots, even that of the largest forms, is not as massive as that of the pigeons. It is somewhat between those of the pigeons and of the Limicolae (Figs. 34, 37). On metacarpus II is a well-developed groove for the tendon of the *M. ext. dig. communis*. The distal process is curved ventrally. At the site of insertion of the tendon of the *M. ext. dig. communis* is a small bony elevation which, however, is too small to be described as a muscular tubercle. Metacarpus III is scarcely longer than metacarpus II, and is narrow and thin, but somewhat broadened at its proximal end. On the dorsal surface of the distal end of the carpometacarpus are two channels for the tendons of the *M. inteross. dorsalis* and the *M. inteross. palmaris*. Usually these channels are completely ossified, i.e., roofed with bone, but once in a while (perhaps in younger specimens) they consist partially of connective tissue (roofed with collagen fibers). Digit I has no trace of a second phalange. The basal phalange of digit II is more massive and broader than that of the Limicolae, but narrower than in the pigeons. Sculpturing on the dorsal surface of this phalange is well-developed. The centers of the two hollows may be perforated, as in the *Lari* for example, but the holes are smaller. The internal index process is larger than that in most Limicolae and perhaps a little smaller than the process in the pigeons. The overall shape of the pollex is similar to the characteristic pollex of the Charadriiformes and very unlike that of the Cuculidae. The second phalange is usually somewhat shorter than the first. In species with a very long 10th primary it may be longer than the basal phalange. Digit III is laterally compressed, with a well-developed process, and thus pigeon-like but not similar to that in the Limicolae.

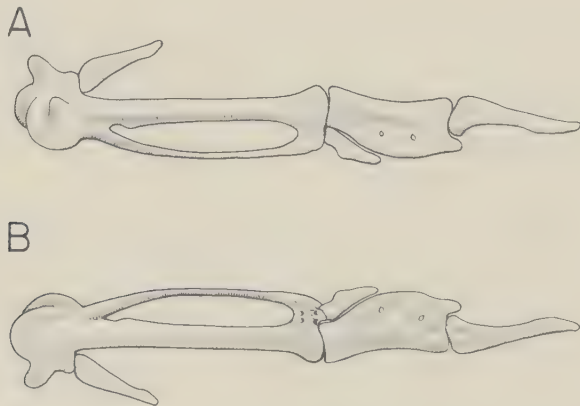


FIG. 34. Manus of *Amazona aestiva*. (A) Dorsum of the skeleton. (B) Venter of the same.

PSITTACIFORMES

The muscles of the wing in parrots (Figs. 35A, B, C, 36A, B, C) do not provide any strong clues to the affinities of this group, although one can see a clear similarity to the musculature of the Laro-Limicolae and of the Pteroclo-Columbae. The tendon of the M. ext. metacarpi radialis is flat and inserts next to the tendon of the M. poll. longus without merging. In this respect parrots are similar to the pigeons and not to the Limicolae. The Lig. humero-carpale is well-developed and the M. flex. dig. sublimis is larger than that in the Limicolae, but smaller than this muscle in the Columbidae.

The M. ulni-metacarpalis dorsalis is small and does not reach beyond the proximal third of metacarpus III, as in the Limicolae. It is, therefore, weaker than this muscle in the Columbidae. The tendon of the M. ext. dig. communis curves sharply before its insertion and is restrained in place by a well-developed loop of the Lig. digito-metacarpale. The M. abductor indicis is larger and long, its tendon curves dorsally before insertion, and it is fixed at the arc with the assistance of the distal process, as is characteristic of the Charadriiformes (Figs. 35A, 36C). The tendon of the M. flex. dig. sublimis inserts on the second phalange of digit II, just as does that of the M. flex. dig. profundus. The M. inteross. dorsalis has the characteristic bipinnate form, as does the M. inteross. palmaris. Both muscles usually reach the distal end of the intermetacarpal space, but they may be shorter in some species.

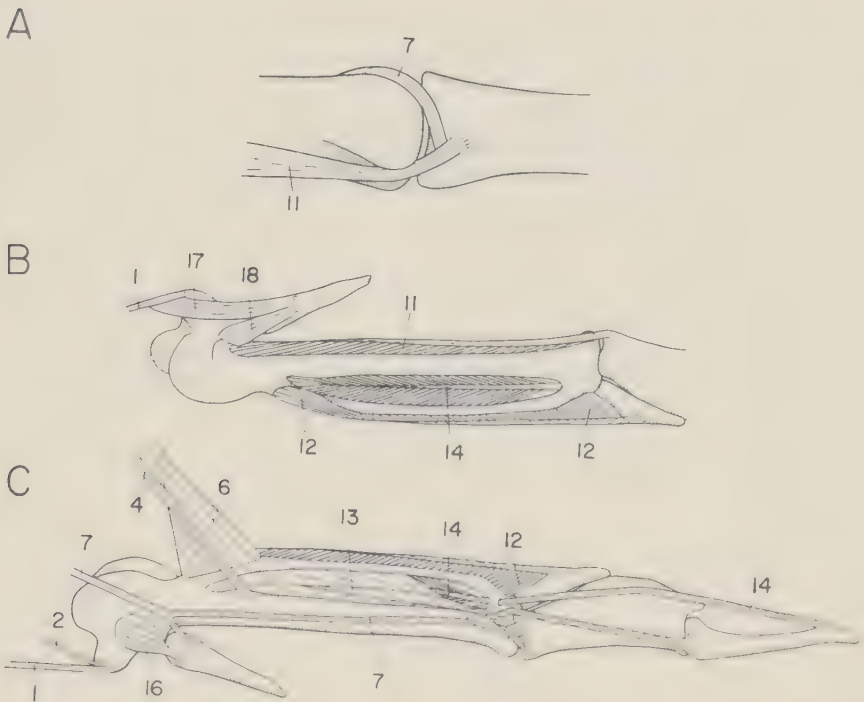


FIG. 35. Manus of *Ara ararauna*. (A) Radial view of metacarpus II. (B) Venter of the musculature. (C) Dorsum of the musculature.

SYSTEMATIC OBSERVATIONS

The structure of these muscles corresponds approximately to those in the Limicolae and are considerably weaker than in the Columbidae. All muscles to digit I are normally developed (Figs. 35B, C, 36A, B).

Discussion.—One may conclude that the morphology of the parrot wing, although not marked by especially characteristic traits, exhibits similarities to only one group of birds. The presence of a well-developed Lig. humero-carpale, and of a weak M. flex. dig. sublimis which arises from it, as well as a well-developed loop of the Lig. digito-metacarpale for restraining the tendon of the M. ext. dig. communis, all clearly indicate that the parrots belong to the Gruiformes-Charadriiformes lineage. Moreover, these features demonstrate that the parrots have nothing in common with the Galliformes-Cuculiformes lineage. Among the Limicolae it is again the most generalized charadriids that show the greatest similarities with the parrots in the anatomy of the wing. The wing characters by which the parrots differ from the Limicolae are similar in the parrots and the pigeons. In some features the parrots are more similar to the Limicolae, while in others they are more similar to the pigeons. From this distribution of features one may conclude that the parrots and the Columbidae evolved in the same direction from a common ancestor, but that the latter group is more advanced.

All of the characters in the structure of the wing that ally the parrots

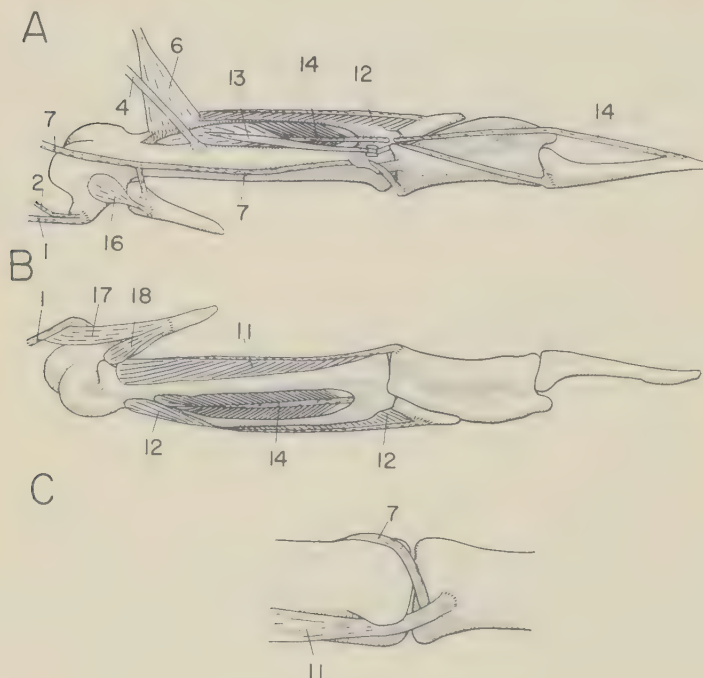


FIG. 36. Manus of *Melopsittacus undulatus*. (A) Dorsum of the musculature. (B) Venter of the same. (C) Radial view of metacarpus II.

with the Columbidae are associated with the peculiarities of their flight. In addition to these similarities are others that are no less important (Stegmann, 1964). These are the unique structure of both the clavicle and the humerus in the Columbidae and the Psittaciformes. These differences are correlated with the strange arrangement of the *M. pectoralis* and the *M. coracobrachialis* anterior, as well as with the peculiar position of the crop. The reason for the evolution of distinctive morphology in this large complex of structures lies in the trophic characteristics of both groups. Those features that conflicted with the method of flight had to be eliminated by evolutionary changes in the morphology of the shoulder. Because the resulting evolutionary changes were the same in both groups it seems probable that the parrots and the pigeons are not convergent toward one another, but rather are closely related groups that have undergone parallel evolution from a common ancestor. The closeness of this relationship is hard to judge.

It is necessary to ask whether it is possible whether the parrots with their uniquely specialized bill could have evolved from such weak-billed forms such as the Limicolae and the Columbidae. First, it must be emphasized that the bill of the parrots is so strongly specialized that no other group of birds comes even close in this respect. The Cuculidae are in no way more similar to parrots in bill structure. Second, it may be concluded that the structure of the bill is especially labile in birds because it is directly adapted to feeding habits. It is, therefore, not especially surprising that the slightly specialized bill of the plovers could have given origin to the strong bill of the Lari, that within the genus *Larus* the strength of the bill is extremely variable, or that within the alcid there can occur two such extremely different bill shapes as exhibited by *Cepphus* and *Lunda*.

The shape of the bill is also highly variable within the Columbidae. The tropical species of the genus *Treron* have stronger bills than the typical pigeons of the genus *Columba*. This is because they pull to pieces their food, which consists mainly of figs. The very aberrant species *Didunculus strigirostris* has a very strong bill with a hook at the tip of the upper jaw. It feeds on seeds with hard shells and nuts, which it gnaws as do parrots.

The highly specialized feet of parrots also do not resemble in any way the weak, little specialized feet of the Columbidae. But those species of pigeons that feed in trees do have a peculiar specialization. Even the Eurasian ringdove is able to hang from thin twigs when collecting acorns (Goodwin, 1967). Many representatives of the subfamily Duculinae are more specialized for life in the canopy. Their legs are short and toes long; the hallux is especially elongated, the claws are decurved and strong, and the underside of the toes are broadened. These birds climb around in the branches when feeding, mainly with the head down, as many parrots do. The pigeons of the genus *Treron* use their bill when climbing, as is characteristic of parrots (Goodwin, 1967). *Treron* pigeons are also vividly green with yellow and red feathers. Other pigeons are mainly blue in coloration. These colors parallel those found in parrots.

At this time I do not wish to claim that pigeons are, in any way, tending

SYSTEMATIC OBSERVATIONS

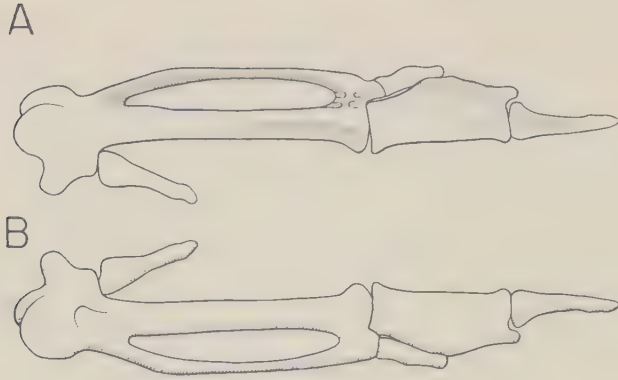


FIG. 37. Manus of *Strigops habroptilus*. (A) Dorsum of the skeleton. (B) Venter of the same.

toward the parrots or that they represent a transition from one group to the other. But one should not underestimate the possibility of extensive variations in the Columbidae. One could logically assume that the primitive members of the pigeons developed a branch that became completely arboreal and from which, over the course of geological time, the present group of parrots evolved. The primitive ancestors of the parrots, however, had to live in trees and feed on plant material. In other words, they had to possess the basic adaptations of pigeons.

The most diverse members of the Psittacidae are very similar to one another in the anatomy of their wings. Neither their systematic position nor their size is correlated with any anatomical characteristics of the wing. Even flightless *Strigops habroptilus* differs very little in wing morphology from other parrots. Its carpometacarpus is relatively shorter than that in its closest relative, *Nestor*, and the second phalange of digit II is especially shortened. But the skeleton of the whole manus is strong and shows no indications of reduction (Fig. 37). The channels for the tendons of the M. inteross. dorsalis and of the M. inteross. palmaris are completely ossified and the ligamentous loop for restraining the tendon of the M. ext. dig. communis is normally developed. The wing is short and very rounded with a shortened 10th primary. This corresponds completely to the proportions in length of the skeleton of the manus and indicates an adaptation for flight in dense forest. Thus the flightlessness of the kakapo seems to be in doubt and it is possible that this bird has retained the ability to at least fly into trees.

SUMMARY

The major goal of this work has been to present a descriptive comparison, as well as a study of the functional anatomy, of the manus of the wing of those birds grouped together by Gadow (1891–1893) as the Alectoromorphae, one of the four great subgroups of carinate birds. Earlier comparative anatomical studies of the distal-most part of the wing are almost nonexistent, but because this portion of the wing provides a large number of taxonomically useful characters, it seemed worthy of greater consideration in order to form an additional basis for systematic study of avian relationships.

Within the Alectoromorphae I have investigated a large number of families and species, some of which have been studied intensively. No major gaps were left unstudied in this segment of our scheme of avian classification. Aside from the value these findings have in providing new taxonomic data, it is hoped that they will serve as an inspiration for further comparative studies on the avian wing.

All phylogenetic conclusions reached in this study are based on study of the manus. Therefore, I do not claim that the proposed systematic classification is the only valid one. It does, however, provide material and ideas for a comparison with the evidence and conclusions drawn from systematic studies of other features.

The basic taxonomic conclusions of this study are as follows:

1. The validity of Gadow's Legion Alectoromorphae is supported by the structure of the manus, with only one modification, viz., that Gadow's Cuculiformes (the current Cuculiformes and the Psittaciformes) should be transferred from the Coraciomorphae to the Alectoromorphae.

2. Based on the evidence presented herein, the Legion Alectoromorphae of Gadow can be divided into two superorders, viz., the Alectoromorphae and the Charadriomorphae.

3. At the base of the Alectoromorphae are the Tinamiformes. Because of the palaeognathous structure of the palate, the Tinamiformes are placed with the several orders of ratite birds and separated from all other modern flying birds. But according to the morphology of the wing, in spite of being very primitive, the Tinamiformes should be placed at the base of the Alectoromorphae. Following the Tinamiformes are the Cariamae even though they are also rather primitive. Following them and more highly developed (approximately at the level of the Galliformes) are the Psophiae. The systematic position of the Cariamae and Psophiae has not been established, but both belong to the Alectoromorphae and not to the Charadriomorphae.

4. The Galliformes represent the central group within the Alectoromorphae. In the Galliformes one can see a clear evolutionary lineage from very primitive forms to those that are very advanced and specialized. The Opisthocomiformes form a side branch from the Galliformes. The Opisthocomiformes are in some respects more advanced than the Galliformes, but in other features they are more primitive. They also have important similarities in common with the Cuculiformes. The Cuculiformes, which includes the suborders Musophagi and the Cuculi, are, in general, more advanced evolutionarily than the Galliformes but they have some very primitive characteristics.

SUMMARY

which means that they cannot be considered simply to be a continuation of the latter group. The Musophagidae and the Cuculidae are clearly more closely related to each other than to any other group of birds and are, therefore, to be kept in a single order.

5. At the base of the Charadriomorphae are the Rallidae, which can be considered to be the most primitive group within the Gruiformes. They are very primitive but already show the main characters of the Charadriomorphae. The Turnicidae are derivatives of rails which became chicken-like in their specialization. The Otidae rank well above the rails, but are surpassed by the Gruidae which constitute the most advanced group of the Gruiformes. The Burhinidae stand between the Gruiformes and the Charadriiformes, and approximately equal the level of organization shown by the bustards.

6. The central group of the Charadriiformes is the Charadrii (Limicolae), which contains primitive, generalized forms as well as highly specialized ones. The Jacanidae form an aberrant group that has much in common with the Charadrii. The Chionidae and the Thinocoridae are more removed, but must still be considered to be related to the Charadrii. The Lari constitute a separate group that branched off from the primitive Charadrii. The Alcae also came off from the primitive Charadrii but they are not directly related to the Lari.

7. The Columbiformes have also branched off from the primitive Charadrii. After they had acquired their general characteristics, another aberrant group, the Pteroclididae, branched off from the main lineage of the Columbiformes.

8. The Psittaciformes branched off from the very base of the Columbiformes and possibly evolved parallel to the pigeons because of similar flight demands, although they did not reach so high a degree of specialization as did the pigeons. This group forms the terminal branch of the Charadriomorphae and has no close affinity at all to the Cuculiformes which are, in turn, the terminal branch of the Alektoromorphae and, therefore, are of a completely different lineage from that of the Psittaciformes.

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